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CONTENTS

WATT—A Mathematical Model for the Effect of Densities of Attacked and Attacking Species on the Number Attacked 129

LILLY—Response of *Limonius californicus* (Mann.) (Coleoptera: Elateridae) to a Sex Attractant Separable by Paper Chromatography 145

PETERSON—Observations on Mating, Feeding, and Oviposition of Some Utah Species of Black Flies (Diptera: Simuliidae) 147

CRAM and TONKS—Note on Occurrence in British Columbia of the Omnivorous Leaf Tier, *Cnephasia longana* (Haw.) (Lepidoptera: Tortricidae), as a Pest of Strawberry 155

HOWDEN—A New Species of *Anoplodera* Mulsant in the *mutabilis-aspera* Group (Coleoptera: Cerambycidae) 157

MUNROE—Pyralidae from the Collection of the California Academy of Sciences (Lepidoptera) 161

CHILLCOTT—The *Pegomyia hyoscyami* (Spinach Leaf Miner) Complex in North America (Diptera: Muscidae) 167

JUDD—Studies of the Byron Bog in Southwestern Ontario X. Inquilines and Victims of the Pitcher-Plant, *Sarracenia purpurea* L. 171

WISHART and RIORDAN—Flight Responses to Various Sounds by Adult Males of *Aedes aegypti* (L.) (Diptera: Culicidae) 181

BOOK REVIEW—Insects and Mites of Western North America 191

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The Canadian Entomologist

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A Mathematical Model for the Effect of Densities of Attacked and Attacking Species on the Number Attacked

By K. E. F. Watt

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Any realistic mathematical model of insect pest population dynamics to be used in maximizing control efficiency must mimic the effects of weather, the habitat, other organisms of various species, food, and chemicals applied by man. However, before such a model can be constructed, suitable mathematical formulations for the mechanism of each type of factor must be developed.

One set of factors which can regulate host or prey survival is the densities of the host or prey, and of its parasites and predators. Such interactions have received more attention from theoreticians than any other problem in population dynamics. A principal aim of this paper is to examine various theories already published in the light of quantitative data available to test them. It will be found that all existing models are inadequate to mimic field and laboratory data; hence a new model will be developed.

This is the first of a series of papers aiming to demonstrate that the dynamics of insect populations can be understood in terms of a small number of simple laws and their interaction. These papers, and companion publications of Science Service personnel collecting data on natural populations will show that apparent differences in the dynamics of various populations are quantitative, not qualitative. That is, an enormous variety of cases of the same phenomenon may be explained in terms of a basic equation merely by altering parameter values.

A logical basis is needed for systematizing the search after most useful biological control agents. A second purpose of this paper is to provide a first step in such a rationale.

Another aim is to demonstrate the usefulness and enormous possibilities of combined inductive-deductive mathematical analysis of existing data, and the structural models so obtained.

Finally, in the following discussion we shall examine the areas of deficiency in our knowledge, and determine how these arose and what can be done to eliminate them.

Assumptions on which Existing Models are Based

We shall now review the assumptions on which certain classical equations were based. Each will be assessed in the light of results from field and laboratory studies. A complete survey of the literature will not be attempted here since several reviews of this area are already in print. (e.g. Andrewartha and Birch, 1954; Milne, 1957; Solomon, 1949; Thompson, 1939; Ullyett, 1953).

In 1922 Thompson published four papers on a theory of insect host-parasite systems. The equation describing parasite increase is of particular concern here. Thompson uses p to denote the initial number of parasites, s for the multiplication of parasites each generation, and f for the proportion of p consisting of females. Then, he says, where the parasite only deposits a single egg in each host, and attacks only unparasitized hosts, there are at the end of one generation p f s parasites.

Now this is perfectly true, but we must also have insight into the nature of s. Subsequent authors, including Thompson himself in later papers, assumed

that the number of hosts attacked per female must be a function of either or both of the host and parasite densities.

In 1923, Lotka published the equation

$$\frac{dN_1}{dt} = bN_1 - dN_1 - aN_1N_2 \qquad (1)$$

to describe the rate of change of host or prey density, N_1, with time. The constants b and d are coefficients of birth and natural death, respectively, and a is a coefficient of attack by a parasite or predator species whose density is denoted by N_2. Our present concern is with the fundamental assumption contained in the term $-aN_1N_2$. This states that the probability of hosts (or prey) being attacked at any instant is proportional to the product of the densities of hosts (or prey) and parasites (or predators). Volterra (1926) independently made the same assumption.

It is now clear that equation (1) does not describe the facts, even approximately, for two reasons. First, the equation implies that an indefinite increase in N_1 will produce a corresponding increase in the number attacked, for constant N_2. This is not so, because the rate of attack per attacker has an upper maximum fixed by egg complement, time-consuming searching behavior patterns (e.g., Dethier, 1957; Edwards, 1954; Laing, 1937; Ullyett, 1936), or digestion rate. Hence, for fixed N_2, increasing N_1 causes the number attacked to rise at a diminishing rate, then level off at some asymptote. This levelling off is graphed by Burnett (1951, 1954, 1958c), DeBach and Smith (1941), Smirnov and Wladimirow (1934) and Ullyett (1949 a,b) and tabulated by Ullyett (1943). Secondly, equation (1) suggests that the attack coefficient is independent of parasite density. Many studies have shown that the number of hosts attacked per parasite decreases with increasing parasite density (Burnett, 1953, 1956, 1958a; DeBach and Smith, 1947; Ullyett, 1949a, b). It is not possible to verify these two points in the field data of Ullyett (1947), Varley (1941) or Walker (1940) because in their studies the effect of N_1 was confounded by N_2. However, it has been possible to sort out the effects of N_1 and N_2 in unpublished data of Miller which were collected according to a sophisticated sampling scheme over many plots and years (Miller, 1955), and his figures confirm the laboratory studies.

Criticisms of the Lotka-Volterra equations have been raised by Andrewartha and Birch (1954), Beverton and Holt (1957), Ivlev (1945), Nicholson and Bailey (1935), Smith (1952), Stanley (1932), Thompson (1939) and Ullyett (1953).

In 1924, Thompson published a different major assumption of insect population dynamics. Where dy/dx represents the rate of change of parasitized hosts with respect to parasite eggs, N represents the initial number of hosts and y the parasitized hosts, he wrote

$$\frac{dy}{dx} = \frac{N - y}{N}, \qquad (2)$$

which integrates to yield the familiar

$$y = N(1 - e^{-x/N}) \qquad (3)$$

The same fundamental idea was presented in different terms by V. A. Bailey in 1931. He considered the gross area s that has to be traversed collectively by the parasites in order that, of u_1 host-eggs initially present per unit area, the number u per unit area remain undiscovered.

The number of previously undiscovered eggs found, while d s is traversed, is u d s. This produces the decrease — du of undiscovered eggs.

Hence $- du = u\, d\, s.$

and $u = u_1^{-s}$.

Now translating this into Thompson's symbols we get

$$N - y = Ne^{-s}$$

$$\text{or } y = N(1 - e^{-s}) \tag{4}$$

If we assume that the number of eggs available for oviposition is proportional to the number of female parasites searching, we can write

$$x = aP, \text{ or } P = a'x.$$

However, if we assume (as Nicholson and Bailey do) that parasites search at random with respect to each other, the area searched will be proportional to the total number of parasites searching, and in turn to the total number of eggs available for oviposition. Hence we may write

$$s = bP = a''x.$$

It is also true that the more hosts there are, the less area each parasite will have to search to lay its complement of eggs. Hence we may write

$$s = \frac{bP}{N} = \frac{a''x}{N} \tag{5}$$

and inserting (5) into (4), we get

$$y = N\left(1 - e^{\frac{-a''x}{N}}\right) \tag{6}$$

which is identical to Thompson's equation; (3), above. (Thompson's equation should have a constant prior to the exponent, to express the efficiency of different parasites). The 1931 Bailey equation is fundamental to the model put forth by Nicholson and Bailey in 1935. Neither Thompson's or Nicholson and Bailey's models incorporate the concept of a limited attack rate and Thompson did not consider a density-dependent attack coefficient. It is noteworthy here that Burnett (1958a, b) has not been successful in obtaining good fits to (3).

Two types of simple tests are available to see if data conform to the assumptions of the Thompson and Nicholson-Bailey models. First, if equation (2) is applicable, then it follows that

$$- \ln (N - y) = \frac{x}{N} - \ln N$$

$$\text{and } \ln\left(\frac{N}{N - y}\right) = \frac{x}{N}.$$

If plotting ln (N/N-y) against x/N does not yield a straight line, we know that eggs were not distributed at random (i.e. the parasites systematically search for unparasitized hosts). Deviations from random searching by two kinds of parasites are illustrated in Fig. 1.

Second, if eggs are indeed distributed at random, Stoy (1932) has shown the distribution formula is

$$Y = N_x C_p \left(\frac{1}{N}\right)^p \left(\frac{N - 1}{N}\right)^{x-p}$$

where Y = the number of hosts with p eggs each, N = the total number of hosts available and x = the total number of eggs to be distributed. The number of ways in which a group of p eggs can be chosen out of a total of x eggs is given by the expression ${}_xC_p$.

Salt (1932) and Walker (1937) showed that *Collyria calcitrator* did not oviposit in accordance with the above formula, and a long list of other studies

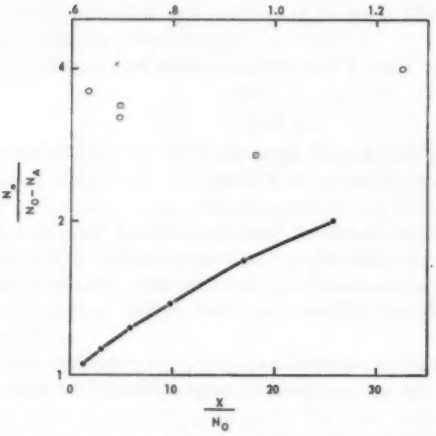

Fig. 1. Deviations from random searching by the chalcid *Dahlbominus fuscipennis* (Zett.) (dots, from Burnett, 1956) and the chalcid *Encarsia formosa* Gahan (circles, from Burnett, 1958a). N_0 represents hosts vulnerable to attack, N_A represents attacked hosts, and x the total number of eggs laid. See text for derivation of equation.

disproving the hypothesis of random searching is discussed by Thompson (1939) and Ullyett (1953).

A third major assumption with regard to the effect of host and parasite densities on hosts attacked was made in 1952 by Bodenheimer and Schiffer in their equation (17). Using the same notation as in (1) above, they stated that

$$dN_1/dt = b_1N_1 - a_1N_2. \tag{7}$$

Equation (7) does not describe the facts for the same reasons that the Lotka-Volterra equation is inappropriate.

Gause (1934) employed a model which incorporated the notion that predators or parasites have some fixed upper potential number of attacks, a. Where y represents the relative increase of predators, and x, the concentration of prey, Gause wrote

$$dy/dx = k\,(a - y) \tag{8}$$

which upon integration yields

$$y = a\,(1 - e^{-kx}). \tag{9}$$

While this equation meets one of the criticisms levelled at the previous models, it is faulty in that it employs a constant rate of attack, k. If Gause's model was correct, then from (8),

$$-\ln (a - y) = -\ln a + k\,x, \qquad \text{whence}$$

$$\frac{\ln\left(\frac{a}{a - y}\right)}{x} = k \tag{10}$$

which is the equation of a horizontal straight line parallel to the axis of abscissas. Several graphs presented hereinafter will show that (10) is not applicable.

A New Model

Before approaching to development of a new model, some comments about this author's model-building technique seem worthwhile.

With regard to general method, a combined deductive-inductive approach is used, rather than relying on pure regression analysis, which is merely an

interpolatory procedure yielding no insight into mechanisms, or pure deduction, which I have criticized elsewhere (Watt, 1956, 1958). Also, to make sure that a structural model is indeed general, it should be evaluated using a great number and variety of bodies of data. Equations (13) to (17) which follow were selected from an array of equations, all somewhat reasonable, and for all of which the basic assumptions were checked against 29 blocks of data. These included eleven cases of laboratory host-parasite systems, nine field host-parasite complexes, eight field predator-prey interactions and one laboratory predator-prey experiment. The aim throughout was to develop a model in which the constants would have intuitively obvious biological meaning. Equation (19) was developed and tested using Miller's data; (21) as yet represents a possibility for which a counterpart has not been found in empirical data.

Definition of Symbols:

N_A the number attacked
N_O the initial number of hosts or prey vulnerable to attack
P the number of parasites or predators actually searching
A coefficient of attack, the N_A per P (an instantaneous rate)
K the maximum number of attacks that can be made per P during the period the N_O are vulnerable.

Since we seek an integral equation of form $N_A = f(N_O, P)$, this could be obtained from a partial differential equation of type

$$\partial N_A/\partial N_O = g_1 (N_O,P) \tag{11}$$

or one such as

$$\partial N_A/\partial P = g_2 (N_O,P). \tag{12}$$

The reason for starting with (11) rather than (12) was that the structure (11) should have was more intuitively obvious. In general, there will probably be more than one road to a complex integral equation, and a large part of the problem of obtaining it has been solved when we have ascertained the easiest route.

Equation (13) states that all parasites or predators can generate a total of PK attacks, and $\partial N_A/\partial N_O$ diminishes gradually as N_A approaches this maximum.

$$\frac{\partial N_A}{\partial N_O} = PA(PK - N_A) \tag{13}$$

However the larger A is, the greater dA/dP will be, because it will be more difficult for parasites or predators to find unattacked hosts or prey. At the same time, dA/dP must decrease in inverse ratio to P, because the greater P is, the greater inter-attack competition will be. This competition might take any form from active interference to superparasitism. The above ideas are expressed in the equation

$$\frac{dA}{dP} = \frac{-bA}{P}$$

$$\text{or } \ln A = \ln a - b \ln P$$

$$\text{or } A = a P^{-b}, \text{ where a and b are positive constants.} \tag{14}$$

Substituting (14) in (13) we get

$$\frac{\partial N_A}{\partial N_O} = P\, a\, P^{-b} (PK - N_A) \tag{15}$$

and integrating,

$$-\ln (PK - N_A) = -\ln PK + N_O P\, a\, P^{-b} \tag{16}$$

which gives

$$N_A = PK \left(1 - e^{-aN_O P^{1-b}}\right). \tag{17}$$

Equation (17) expresses the numbers attacked in terms of the numbers of parasites or predators actually searching. However, in many field studies on parasites, this variable can never be measured, for technical reasons. In such cases, it is typically possible to measure P_p, the number of parasites present in the previous generation. Now it will often be true that the most important factor in determining the number of parasites surviving, P_s, will be N_{Op}, the number of hosts in the previous generation. We may write

$$\frac{dP_s}{dN_{Op}} = -cP_s$$

$$\text{or } \ln P_s = \ln P_p - cN_{Op}$$

$$\text{and } P_s = P_p e^{-cN_{Op}} \tag{18}$$

Inserting (18) into (17), we get

$$N_A = P_p e^{-cN_{Op}} K\left[1 - e^{-aN_O(P_p e^{-cN_{Op}})^{1-b}}\right] \tag{19}$$

A still further level of complexity will be encountered in cases where K is density-dependent and we get

$$\frac{dK}{dP} = -dK$$

$$\text{or } \ln K = \ln f - dP \text{ and}$$

$$K = f e^{-dP}. \tag{20}$$

Inserting (20) into (19) we get

$$N_A = P_p e^{-cN_{Op}} f e^{-dP_p e^{-cN_{Op}}}\left[1 - e^{-aN_O(P_p e^{-cN_{Op}})^{1-b}}\right] \tag{21}$$

It is known that the various constants in (21) can be modified by the action of weather and other environmental variables. For example, Burnett (1951, 1953, 1954, 1956) has shown in a series of papers that K and a can be modified by temperature.

Empirical Verification of the Above Equations

This author has conducted a search of both published data and material loaned him by research officers of the Canada Department of Agriculture to determine if equations (13) to (21) describe all field and laboratory findings. It is extremely noteworthy that few bodies of data have ever been collected and analyzed in a manner allowing one to both critically check these assumptions and develop a more realistic model if this seemed necessary.

One or more of five basic defects has been present in most studies done on this problem.

First, either the design of the sampling plan, or the volume of replication has often been inadequate to avoid having sampling error or confounding by unmeasured variables obscure the basic principles at work to generate the data. (A cogent criticism of economic entomologists' sampling is given by Milne, 1957).

Secondly, in many field studies, not enough variables are measured. Typically, people working on predators record only N_O and P, and observers of parasite-host systems count only N_O and N_A. In the case of predators, N_A may be counted directly if the predator leaves some evidence (eg. woodpecker holes). If N_A cannot be counted directly, it can be estimated from the difference between N at different times, at each of several sampling sites. The sampling scheme must be designed to allow separation of changes in N due to changes in fecundity and non-predator-induced mortality from mortality due to preda-

tion. Researchers studying field parasite-host systems can estimate P from P_p, as mentioned previously. This implies that a study should be continued at the same sampling sites for many years.

Thirdly, in all studies without exception to date, the researcher has presented his data in the form of one variable, N_A, expressed as a function of either N_0 or P. As far as this author has been able to determine, no empirically based paper has ever been published in which the joint effect of N_0 and P on N_A was explored. An intuitive insight into the meaning of the word "joint" as used in this context may be obtained from chapter 21 in Ezekiel (1942).

Fourthly, only in a very few laboratory cases to date have N_0 and P been allowed to vary at once. Typically, in laboratory studies they are varied one at a time, and in field studies P is not measured. It can be obtained by collecting data from a wide variety of habitats over a long period of years. The Green River spruce budworm study (Morris and Miller, 1954) is the classic in this regard.

Fifthly, laboratory studies on P, N_0 and N_A rarely test the effects of enough different values for P and N_0. The pitfall here may be explained simply as follows. Obviously any curve can be fitted to two points. In general, the less points one has, and the narrower the range of values one has, the more difficult it becomes to discriminate between the applicability of different hypotheses. An excellent discussion of this point is in Hald (1952, pp. 558-570). For example, unless values of the transformation in equation 24 which follows are spread over a very wide range, great changes in K are required to produce much bending of the line described by (24) on log-log paper. Hence it is difficult to estimate K accurately unless a wide range of P values was included in the original experiment.

While the data already available do not allow us to know if we have built a completely satisfactory model showing how N_0 and P govern N_A, they have allowed us to develop a model which fits the observed data more closely than those already in the literature.

There are at least three different methods that could conceivably be followed in fitting curves such as (21). One could use a non-parametric multivariate approach, but neither this author nor various statisticians with whom he has discussed the matter could see any advantage here. Secondly, one could use an extension of the maximum likelihood procedure outlined by Stevens (1951). Finally, and this seemed best for a variety of reasons, simple least squares methods can be modified. In this case, it may be necessary to use weights if the assumptions of normality and homoscedasticity have to be relaxed (David and Neyman, 1938). Examples of this weighting procedure are given by Anderson and Bancroft (1952, pp. 182-186).

The simplest type of data to fit are those from laboratory experiments in which only N_0 was varied. From (16),

$$\ln \frac{PK}{PK - N_A} = N_0 (aP^{1-b}). \qquad (22)$$

Since P is held constant, the aP^{1-b} term may be considered constant, and values for K and $A = aP^{1-b}$ may be obtained through regression methods. The calculation is illustrated in Table I using data of Debach and Smith (1941).

The number 63 was obtained by trial and error (the appropriate value is that which straightens the line in Fig. 2). The values of $63/(63-N_A)$ are plotted against N_0 on semi-log paper in Fig. 2. The constants may be obtained

directly from such a graphical procedure. However, if a more precise estimate of K and A is desired, we can select the value of K that minimizes the residual sum of squares (or maximizes the correlation coefficient) for the regression of ln (PK/PK—N_A) on N_O. Here, we found from Fig. 2 that PK was 63; since P was 40, K was 1.6 (to the first decimal).

TABLE I
Results of search by 40 parasites for hosts in varying densities

Host Density N_O	Hosts Attacked N_A	$PK - N_A$	$\frac{PK}{PK - N_A}$
1	.89	62.11	1.01
5	4.00	59.00	1.07
25	17.57	45.43	1.39
50	31.50	31.50	2.00
100	48.25	14.75	4.27
200	54.25	8.75	7.20
300	62.00	1.00	63.00

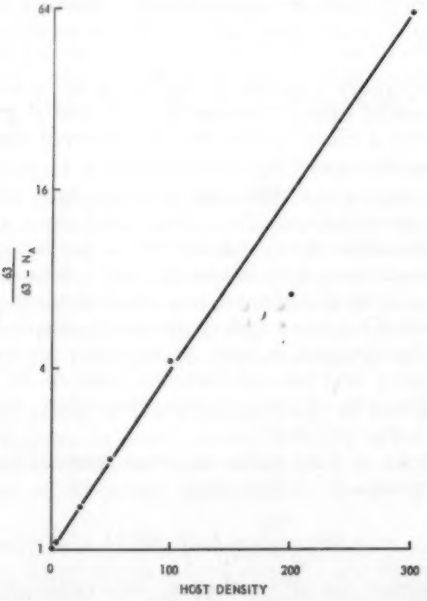

Fig. 2. Searching by *Nasonia vitripennis* (Walker) for puparia of the housefly, *Musca domestica* L. Figure 2 tests the hypothesis that ln $PK/(PK—N_A) = AN_O$, where PK, here equal to 63, is maximum number of hosts all parasites can attack, N_A is hosts attacked, and N_O denotes initial host density. The aberrant point has a very low weight relative to points near the origin. Weighting was by the number of replications divided by the variance. Data from DeBach and Smith (1941).

The data of DeBach and Smith are for the chalcid, *Nasonia vitripennis* (Walker), searching through ten-gallon tins of barley for puparia of the housefly, *Musca domestica* L. Much more convincing evidence for the validity of equation (13) comes from field studies where the conditions are more natural. For example, Burnett (1954, 1958c) has studied the effect of varying densities of cocoons of *Neodiprion lecontei* (Fitch) being sought for by the chalcid *Dahlbominus fuscipennis* (Zett.) on a lawn and in a mixed wood plot. The relevant data transformed according to (22) are given in Figs. 3 and 4. Lines I, II and III in Fig. 4 represent three different experimental designs, and sets of weather conditions. The most convincing confirmation of (13) this author has seen yet comes from the data of Miller (ms. in preparation). His data come from several forest stands over an eight year period and cover a very wide range of values.

The transformation required for rectilineation of laboratory experiment data where only P was varied is somewhat more complex. From (22),

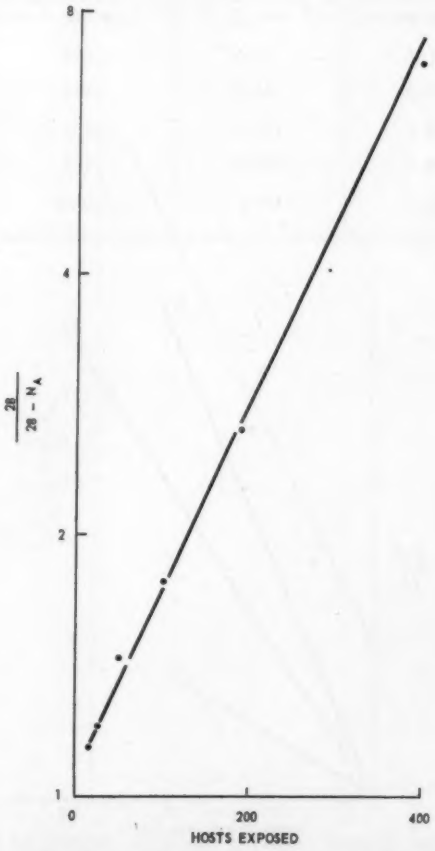

Fig. 3. Searching by *Dahlbominus fuscipennis* (Zett.) for *Neodiprion lecontei* (Fitch) on a lawn, (Burnett, 1954). Test for same hypothesis as in Fig. 2.

$$\ln \frac{\frac{PK}{PK - N_A}}{N_0 P} = aP^{-b} \tag{23}$$

which becomes susceptible to linear regression in the form

$$\ln \left[\ln \frac{\frac{PK}{PK - N_A}}{N_0 P} \right] = \ln a - b \ln P. \tag{24}$$

TABLE II
Results of search by variable number of parasites for 40 hosts (K = 1.70)

Parasite density P	Number of hosts attacked N_a	$PK - N_a$	$\ln \frac{PK}{PK - N_a}$	$\ln \frac{\frac{PK}{PK - N_a}}{N_0 P}$
5	8.4	.1	4.44	.022
25	21.1	21.4	.688	.000,69
50	31.2	53.8	.457	.000,23
100	38.2	131.8	.255	.000,064
200	40.0	300.0	.125	.000,016
300	40.0	470.0	.0815	.000,0068

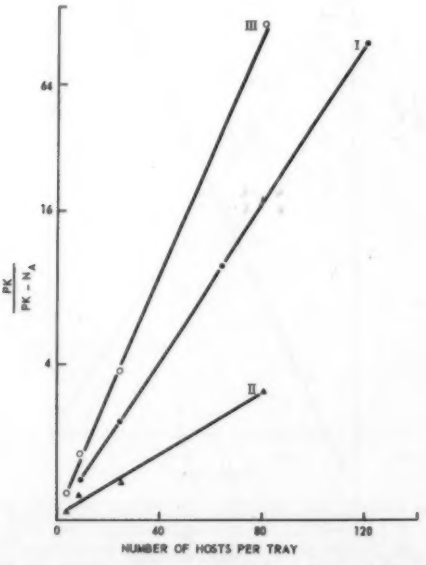

Fig. 4. Searching by *Dahlbominus fuscipennis* (Zett.) for *Neodiprion lecontei* (Fitch) in a mixed wood plot (Burnett, 1958c). Test of some hypothesis as in Fig. 2. The three lines are for three different combinations of weather and parasite and host densities.

The data of DeBach and Smith (1947) are transformed according to (24) in Table II; graphical estimation of K, a and b may be done using log-log plots as in Fig. 5. Again, the most precise estimates of the constants may be obtained by seeking the value of K which maximizes the correlation coefficient.

A large number of confirmations of (15), using the transformation in (24), would be required to constitute a really convincing case. Fig. 6 shows data of Burnett (1956) on *D. fuscipennis* searching for *N. lecontei* over a lawn. The horizontal segment at the upper end shows up in Burnett's corresponding laboratory study (1953). This occurs because *D. fuscipennis*, according to the outcome of these experiments, does not search at all unless it is present at densities greater than a minimum threshold value. Fig. 7 describes searching of the chalcid *Encarsia formosa* Gahan for the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.) in a greenhouse (Burnett, 1958a). Figs. 8A and B present the results of two experiments by Ullyett (1949a, b). In the first, the braconid *Chelonus texanus* Cress. is searching for eggs of the flour moth, *Anagasta kühniella* (Zell.) in Syracuse watch glasses. In Fig. 8B, the results are transformed according to (24) for the ichneumonid *Cryptus inornatus* Pratt hunting for cocoons of *Loxostege sticticalis* (L.), the beet webworm.

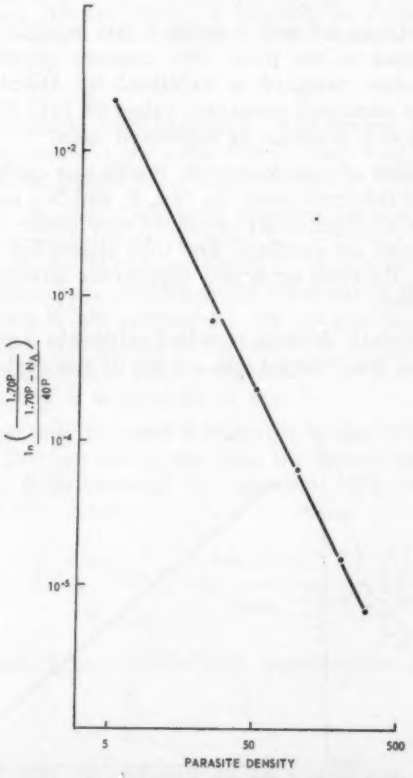

Fig. 5. Searching by *Nasonia vitripennis* (Walker) through ten-gallon tins of barley for puparia of the housefly, *Musca domestica* L. (DeBach and Smith, 1947). Figure 5 is a test of equation (23) in the text. The symbol P represents parasite density, and other letters are defined as in text and Fig. 2 caption.

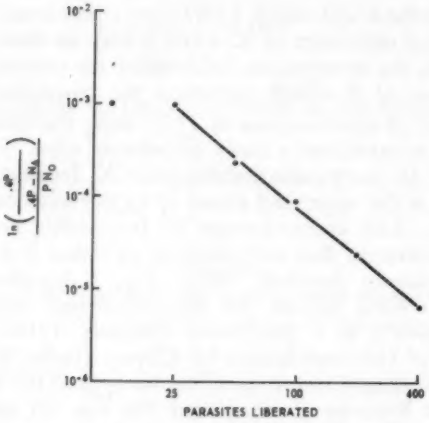

Fig. 6. Searching by *D. fuscipennis* for *N. lecontei* over a lawn (Burnett, 1956). Remarks same as for Fig. 5.

The next type of case we shall consider is that in which N_O, N_{Op}, P_p and N_A have all been measured in the field. We concern ourselves here only with the apparent N_A value, measured as explained by Miller (1955). Since the complete routine for obtaining parameter values in (21) is rather involved, we shall outline it here as a sequence of numbered steps.

Step 1. Prepare a deck of punched cards, needle-sort cards, or hand-sort cards on which are entered reference data, N_O, N_{Op}, P_p and N_A, for each plot and year. (Canada Department of Agriculture personnel may obtain hand-sort cards from the author. Two sizes are available: one with spaces for 18 variables and one with spaces for 38. Punched cards and appropriate auxiliary equipment should be used for large jobs).

Step 2. Divide the whole deck of punched cards into a convenient number of sub-decks, sorting on the variate-value for P. If the deck is small (under 100

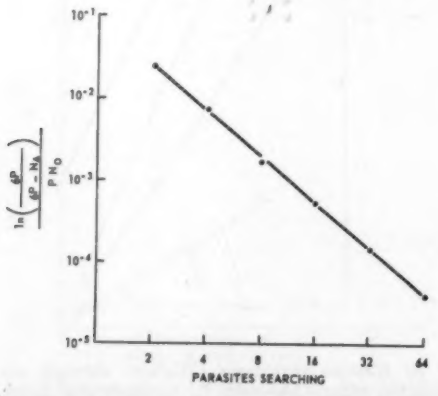

Fig. 7. Searching by *Encarsia formosa* Gahan for *Trialeurodes vaporariorum* (Westw.) in a greenhouse (Burnett, 1958a). Remarks same as for Fig. 5.

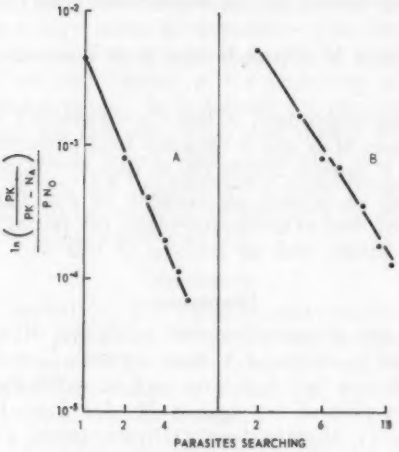

Fig. 8. A. Searching by *Chelonus texanus* Cress. for eggs of *Anagasta kühniella* (Zell.) in Syracuse watch glasses (Ullyett, 1949a). B. Searching by *Cryptus inornatus* Pratt for cocoons of *Loxostege sticticalis* (L.) (Ullyett 1949b). Symbols have same definitions as for previous figures.

cards), only three sub-decks should be used. The sorting may conveniently be done by ranking the cards on the value for P_p, then making the subdecks out of the first n/3 cards, the second n/3, and the third n/3, where n is the deck size.

Step 3. For each of the three sub-decks calculate the correlation coefficient r as a function of K, for an array of values of K. The best values of K, a and b are those obtained with the K that maximizes r. A worksheet is available from the author. Two other types of information come out of this analysis. First, if the curves of r against K are multimodal, we are pooling heterogeneous plots and/or years. Second, if the curves for different ranges of P_p values have different maxima, we know K is density-dependent. If K is not density-dependent, proceed to step 4; if it is, proceed to step 5.

Step 4. The equation now obtained is incorrect in that it does not account for parasite mortality. We can obtain the term for this as follows. Suppose our N_A calculated, N_{Ac}, is represented by equation (17), while N_A observed, N_{Ao}, is denoted by (19). Then

$$\frac{N_{Ao}}{N_{Ac}} = \frac{P_p e^{-cN_{Op}} K\left[1 - e^{-aN_O\left(P_p e^{-cN_{Op}}\right)^{1-b}}\right]}{P_p K\left[1 - e^{-aN_O P_p^{1-b}}\right]} \tag{25}$$

and at low N_{Op} values, a very satisfactory approximation is

$$\frac{N_{Ao}}{N_{Ac}} = e^{-cN_{Op}}. \tag{26}$$

The constant c may be obtained either graphically, from a plot of ln (N_{Ao}/N_{Ac}) against N_{Op}, or from an algebraic regression analysis if the biological data warrant a high degree of computational precision (generally they won't). In either case, the value of c would only be obtained from the part of the line

prior to the curvature caused by the exponential term exp $(-cN_{op})$ in the numerator of (25).

Once a value for c is obtained, step 3 is repeated, substituting P_p exp $(-cN_{op})$ for P_p.

Step 5. If K is density-dependent, obtain the constants f and d from equation (20), using paired values of K and P obtained from different curves of r against K for three or more P density ranges (as in step 3). Then proceed to step 4.

There is no need to present an example of the above calculation here. Possibly the best set of data available anywhere for testing this model has been collected by Charles Miller, and an analysis of this data will be presented in another paper.

Discussion

It was stated in the introduction that a variety of apparently discrepant cases can be explained in terms of a basic equation merely by altering parameter values. It will now be clear how such superficially dissimilar cases can arise. For example, a plot of N_A against N_O for fixed P may be rectilinear (Burnett, 1958b, Fig. 1), slightly bent (Ullyett, 1949a, Fig. 2), or a sharply bent line approaching an asymptote (DeBach and Smith, 1941, Fig. 1). The lower PK is relative to the array of N_O values tested, the greater the bending will be. Similarly, a plot of N_A against P will have different shapes depending on the size of the coefficients a, b and K.

Equation (14) is of interest in two connections.

First, Emerson (in Allee et al, 1949, beginning page 698) has given a long, closely reasoned argument that "interspecies associations evolve as supraorganismic units". The point of (14) is that parasites become less effective per head if their density increases, and hence have a built-in mechanism to prevent annihilation of the hosts, their food. The mechanism works against the short-term interests of the parasites, but for the long-term interests of both parasites and hosts. We would expect such a mechanism if natural selection had been operating on the host-parasite complex as an integrated unit.

Second, an analogous situation to that of entomophagous insects searching for their hosts or prey is that of men fishing (preying systematically) on fish. Data for the effect of number of anglers per boat on fish caught per angler per rod-hour (Watt, 1959) give the form $dA/dP = -bA$, rather than (14). Clearly, P will only appear in the denominator of the differential equation when there is some form of real competition between predators.

This paper constitutes a first step in providing a logical basis for systematizing the search after most useful biological control agents. The most effective parasites or predators at times of low host or prey density are good searchers with high a values. At pandemic host levels, the best entomophagous insects are those with high biotic potentials (f) and low coefficients of response to high host density (c) and parasite density (b, d). After further research on a variety of cases, it should be possible to express each of these coefficients in terms of measurable biological parameters. It is to be hoped that at that time, the potentialities of structural mathematical models for economic entomology will have become eminently clear.

Possibly the most basic conflict of opinion amongst population ecologists concerns the pragmatic reality of the steady state concept. Volterra (1926), Nicholson and Bailey (1935) and Beverton and Holt (1957) have all built their models around this idea. That is, they explore the long-term average consequences of certain conditions, assuming all other environmental variables to be

constant over time. This author considers such a theoretical approach to be satisfactory only for a very stable environment. For the less stable situations, population consequences in a short period should be expressed in terms of the variate-values of the relevant factors at the beginning of the period, not the long-term average variate values. It is difficult for this author to see the meaning of a "steady state" for fish population year classes which vary 100-fold or insect population year-classes which vary 10,000-fold in response to short-term environmental fluctuations. An implication of these remarks is that the simple models herein may have to be modified considerably to be applicable in specific instances, as noted following equation (17).

Summary

The assumptions underlying five classical mathematical models of host-parasite and predator prey population dynamics are inadequate to account for published data. A new model has been developed and tested against available data. Methods of obtaining parameter values for the model from field and laboratory data are outlined and illustrated.

Acknowledgments

I am indebted to Dr. G. B. Oakland, Mr. C. Reimer, and Dr. W. R. Thompson for a critical reading of the first draft of this paper.

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Response of Males of *Limonius californicus* (Mann.) (Coleoptera: Elateridae) to a Sex Attractant Separable by Paper Chromatography[1]

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In the course of recent field studies in southern Alberta on the behaviour of adults of the sugar-beet wireworm, *Limonius californicus* (Mann.), it has been observed that the males spend much of their time after emergence resting on small clods of earth with their heads pointed upward into the breeze and with their antennae waving as though testing for odours. When they appeared to scent a female they moved into the breeze, crawling or flying, depending on the velocity of the wind. As they neared the female they became increasingly agitated, but when in close proximity to her they seemed confused and often passed within an inch of her. Eventually one of them located her and mating occurred almost immediately. The remaining males finally dispersed after crawling repeatedly around and over the copulating pair. These observations suggested that the females, soon after emerging, release a sex attractant.

Shirck (1942) observed that, in Idaho, males of *L. californicus* were attracted in numbers to each newly emerged female. Lane (1933) reported that female elaterids in traps attracted large numbers of males until the general emergence of females occurred in the field. Travis (1939) suggested that female June beetles released a sex attractant and found that in a breeze males on the leeward side of one of them would come from 30 to 40 feet. Makino *et al.* (1956) isolated a sex attractant from the silkworm moth, *Bombyx mori* (L.), and were able to separate it on a chromatogram using a bioassay technique.

On several occasions during the 1957 flight period of *L. californicus* in Alberta, gravid females of this species were crushed in 70 per cent ethyl alcohol and the resulting crude extract was exposed to male beetles in the field. It provoked no observable response from them.

Early in the flight period in 1958, however, two female beetles were found dead on the soil surface. Because of the fresh, unrubbed condition of their body hair, they appeared to be newly emerged specimens. A male approached one of them with his antennae waving rapidly, as though excited, which suggested that they might have been unmated females still in possession of their attractant. In the laboratory they were torn apart and crushed in 12 mls. of 70 per cent ethyl alcohol. When microscope slides were moistened with the extract and placed in the infested field, within ten seconds numerous beetles from as far away as 40 feet began to move rapidly toward them, crawling and flying excitedly. They remained at the source of the odour for some minutes, crawling over the slides with their antennae waving, and extruding their genitalia repeatedly. A 1:10 dilution of the original extract also attracted males, although in smaller numbers. In a laboratory test the head, thorax, and abdomen of a receptive female were crushed separately in ethyl alcohol, and only the extract prepared from the abdomen attracted males. In the field all males that responded to the extract came against the breeze, and their actions in all tests were very similar to those exhibited by males approaching receptive females. Ethyl alcohol alone induced no response.

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After the original extract had been stored for more than a month at room temperature, it was chromatographed and bioassayed. Paper chromatograms were prepared with the following solvents: NH_4OH (0.1 N), $EtOH.NH_3$ (95:5), HCl (0.1 N), and acetone-H_2O (50:50). After development, each chromatogram was placed at room temperature with 10 males of *L. californicus* in a glass-covered, rectangular container, the base of which was approximately twice the area of the chromatogram. The males had been stored for several weeks in moist soil at 37° F.

The test beetles soon became active at room temperature but showed no positive reaction to the chromatograms until the latter were thoroughly dampened with a fine spray of distilled water. Then their actions toward the chromatograms that had been developed with NH_4OH and with $EtOH.NH_3$ became typical of those displayed by males toward the crude extract. They finally congregated on the paper largely within an area 1½ inches in length. Rf values of about 0.9 and 0.85 were thus obtained from the chromatograms developed with NH_4OH and $EtOH.NH_3$, respectively.

HCl was not a suitable solvent for use with this bioassay technique; the males exhibited great agitation when in contact with the moistened, treated paper and repeatedly tried to clean their antennae by pulling them between their tarsi. Chromatograms prepared with acetone, while not causing the males any evident discomfort, elicited no typical response from them. When butyric acid, one of the fatty acids reported by Lehman (1932) to be attractive to this species, was co-chromatographed with the attractant, the beetles showed no observable reactions to the butyric acid, which has a lower Rf value than that of the extract.

With the limited amount of extract and the small number of unmated female click beetles of *L. californicus* available, it was not feasible to isolate and determine the nature of the attractant. The crude extract, however, because of its specificity of appeal and its stability, may be a useful means of surveying for this species where its population density is low. In one instance males were attracted in a field that had no previously recorded history of sugar-beet wireworm infestations. The extract may also be of value in studying flight behaviour and adult dispersal and in reducing subsequent wireworm populations by attracting the males to traps.

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Observations on Mating, Feeding, and Oviposition of Some Utah Species of Black Flies (Diptera: Simuliidae)[1]

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The literature contains numerous references to observations and investigations on various aspects of the biology of many species of black flies. During recent studies on the blackfly fauna of Utah, observations were made on mating, feeding, and oviposition of several species of black flies for which such data are fragmentary or completely lacking.

Mating

Mating swarms of male black flies have been reported in the literature for a number of species but in only a few species has copulation been seen. In the present study, actual mating was observed only a few times; however, swarms containing both sexes, which were possibly mating flights, were noted for several species.

On May 23, 1958, at the head of Weber Canyon, Weber County, a small number of flies were observed in a rather compact swarm. They were flying about six to 12 inches above a small stream and to the north of the bridge that crossed the stream. They flew back and forth across the stream several times before a sweep net was passed through the swarm. The sweep provided six males and two females of *Prosimulium exigens* Dyar and Shannon and one male of *Prosimulium* sp. 199, a species that will be described as new. This may have been a mating swarm because of the preponderance of males, although no actual coupling was seen.

Reports on the mating behaviour of *Eusimulium canonicolum* Dyar and Shannon are lacking. Adults of both sexes were collected on July 6 and 13, 1956, at Beaver Creek, near Kamas, Summit County. On both occasions the adults were observed in swarms flying two to three feet above a smooth water surface. These may have been mating flights as evidenced by the nearly equal numbers of both sexes in the swarms. Although flies were seen to come together, no actual instances of copulation could be determined.

Mating of *Simulium arcticum* Malloch was observed twice over the headwaters of the Provo River, just below Tryol Lake, Summit County. The first instance occurred at 2:30 p.m. on September 11, 1956, when thousands of flies of both sexes appeared as a haze over the water as they flew up and down along the stream. Several hundred flies were collected with just a few passes of an insect net over the stream. Above numerous, low-flying, ovipositing females were other flies that darted and hovered in an upstream direction three to four feet above the water surface. Numerous pairs of flies were observed in copulation as they flew an irregular course up and down stream. The mating flies remained together for only a short period of time after which the females appeared to join those that were depositing their eggs into the water. A number of pairs of copulating flies were netted, but the flies separated as they were placed in a cyanide killing jar. No mating was observed among flies not in flight.

The second occasion on which mating was observed in *Simulium arcticum* occurred in the same locality on September 1, 1957. Much the same behaviour was noted and again there were low-flying, ovipositing females and higher-flying

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members of both sexes. The flies were much less numerous on this occasion but a number of pairs of coupled flies were netted. Male and female flies were placed in four-dram vials and returned alive to the laboratory. The gravid females laid a number of eggs on the sides of the dry vials. In the laboratory, live flies were inactivated by placing them for a very short time in a cyanide jar. The genitalia were crushed on slides and examined under a compound microscope. Active spermatozoa were observed both in the spermathecae of the females and the testes of the males. Thus it appears that mating in *S. arcticum* can occur just prior to oviposition, as was found to be the case for *Simulium decorum* Walker by Davies and Peterson (1956).

Feeding

Females of many simuliid species feed on the blood of homoiothermous animals to provide the necessary nutrients for ovarian development. Females of some species are not known to feed on blood while others are morphologically incapable of doing so. Males of all known species are non-biting. However, both male and female black flies feed on the nectar of flowers to provide energy for flight and other metabolic processes.

Of the eight species of *Prosimulium* in Utah, none are known to suck blood in this region. Although *Prosimulium exigens* is widespread throughout Utah and the western United States, there are no records of the species biting. Hearle (1932) mentioned that this species (which he cited as *P. dicentum* Dyar and Shannon) was scarce in collections made on the wing or from animals in British Columbia. However, females of *P. exigens* occasionally have been collected flying about the writer. On May 31, 1956, in Chalk Creek Canyon, Summit County, small numbers of females flew into the ears, corners of the eyes, and landed on the author's bare arms. The time was 3:00 p.m., the day sunny, with an air temperature of 75° F., and a light wind was blowing. These flies were annoying but not a single bite was inflicted. Many collected flies contained nectar but none have been found engorged with blood. This may be due to the fact that the larvae store considerable quantities of nutrients which probably become available to pupae and adults. Larvae of *P. exigens* are almost always found in streams with a high content of organic matter and they have a large, conspicuous, yellowish fat-body that fills most of the posterior portion of the abdomen.

In Utah, adult females of *Eusimulium canonicolum* frequently were attracted to the writer but only once, near Brighton, Salt Lake County, at an elevation of 8,730 feet, was one observed biting. A female was taken after a three-minute engorgement on the forearm of a companion. The affected individual complained of the pain of the bite, but little bleeding followed. *Eusimulium canonicolum* (as *E. clarum* Dyar and Shannon) has been reported to feed on birds (Hearle, 1932; Fitch *et al.*, 1946).

Although *Simulium arcticum* has been reported as primarily attacking cattle and other domestic animals, it has been observed to feed on man. The writer collected females of this species as they were feeding on his arms. In Utah, *S. arcticum* has been known to bite man only at elevations above approximately 7,000 feet; most bites received by the author occurred at an elevation of about 10,000 feet near Tryol Lake. The writer also collected a few females as they were biting during a dark night with a fine drizzling rain in the same general region. These flies were collected in association with biting females of *Cnephia mutata* (Malloch), *Simulium hunteri* Malloch, *S. tuberosum* (Lundström) and *S. vittatum* Zetterstedt. The reason why these flies apparently bite only at

altitudes approximating 7,000 feet and higher remains unknown. On September 11, 1956, large numbers of females and males were observed in mating and oviposition swarms over the headwaters of the Provo River. Although many females landed on the author none attempted to bite. Some of the gravid females collected contained blood and nearby workmen informed the author that they had received many bites from "gnats" earlier in the day.

A few females of *Simulium arcticum* were noted flying about the author and a companion while they were hunting deer on October 20 and 21, 1956, in Dutch Canyon, Wasatch County, at an elevation of 9,500 feet. The flies appeared just after sun-up and remained a constant annoyance until sun-down. Females landed on the red caps and shirts, and crawled over the necks and foreheads of the two men. Although no bites were received by either man, two of the females collected contained blood. The flies had probably been feeding on the numerous mule deer (*Odocoileus hemionus hemionus* (Rafinesque)) that were in the area, because all cattle and sheep had been removed from the canyon several weeks prior to the deer hunting season.

The female of *Simulium arcticum* is a vicious biter of livestock and has caused tremendous losses in regions of Saskatchewan, Canada (Cameron, 1918; Millar and Rempel, 1944; Rempel and Arnason, 1947). The flies have been observed by the writer and others to congregate on the less hairy (or possibly more shaded) portions of the animals, such as the undersurface of the abdomen, the inguinal region near the udder in cows and on the scrotum of bulls, as well as just behind the front legs and on the neck region. Rempel and Arnason (1947) mentioned that these flies do not attack livestock to any extent on the facial region. However, the present writer has removed females of *S. arcticum* from the back and inside of the ears of horses and of a few calves in the Salt Lake Valley. On one occasion, ten female flies were removed from the inside of a horse's ear. The flies apparently caused severe irritation as the ear was red and bleeding. Knowlton and Maddock (1944) collected dozens of feeding females of *S. arcticum* and a few females of *S. vittatum* from the head, neck, shoulders, back and front legs, from the brisket and under the belly, as well as from the inside of the ears of horses near the Monte Cristo Forest Camp, Cache County. Rempel and Arnason (1947) also reported that *S. arcticum* would attack sheared sheep and, to a lesser extent, hogs. The writer has collected this species feeding on a dog. Although *S. arcticum* is widely distributed in Utah, it has not been observed to occur in numbers large enough to constitute a serious problem to either man or livestock. However, it may at times be an annoying pest in local areas.

On September 1, 1957, at an elevation of 8,000 feet in the Uinta Mountains of Utah, many adult females of *Simulium hunteri* flew around and landed on the author while he stood in tall, dense vegetation. Large numbers of these flies flew into the author's eyes and ears, and crawled down the back of his neck. Several bites were received on the cheek. A number of females inserted their mouthparts into the grey sweater worn by the writer. Several of these females seemed to have difficulty withdrawing their mouthparts from the sweater as was evidenced by their vigorous shaking and back treading motion. More flies were attracted to the author when he stood in the shade. On several other occasions, *S. hunteri* has been collected while flying about the author both in the Uinta Mountains and the Wasatch Mountains, but few have attempted to bite. A few females of *S. hunteri* were collected near Tryol Lake as they were biting the

writer on a dark July night in 1952, during a light rain. Hearle (1932) reported that this species attacked horses, cattle, and man in British Columbia.

Simulium jacumbae Dyar and Shannon has not been observed to bite in Utah. However, several gravid females collected on September 11, 1956, from oviposition swarms over the upper Provo River, contained blood.

To the author's knowledge there are no published records of *Simulium trivittatum* Malloch feeding on man. This species has not been observed to feed on man in Utah, but was collected on several occasions flying about the author in the southern irrigated desert regions of the state.

Biting females of *Simulium tuberosum* were collected by the author in Utah near Tryol Lake, July 25, 1952, at an elevation of 10,000 feet. This species also was taken while biting on several other occasions in the Uinta Mountains. Females of *S. tuberosum* have been collected at elevations as low as 2,500 feet but none have been observed to bite man below approximately 7,000 feet. On June 9, 1956, females were very bothersome to fishermen on the Strawberry River, Wasatch County. Many flies were collected as they darted into the ears, corners of the eyes, and under the collar and hatband of the writer. The annoyance by these flies began shortly after 6:00 a.m. when the sun was up. The flies, although not biting, were present in sufficient numbers to force many fishermen to leave the river. *Simulium tuberosum* apparently will attack other mammals besides man. Peterson (1956) reported that it fed on ground squirrels, and it was reported to be a pest of cattle, dog, and man in Great Britain (Edwards, 1915; Smart, 1944). *Simulium tuberosum* was reported to feed on humans in the Adirondack Mountains by De Foliart (1951) (as *S. perissum* Dyar and Shannon), and by Jamnback (1952). Davies and Peterson (1956) observed that this species did not bite man or animals in Algonquin Park, Ontario.

Table I presents a summary of published and previously unpublished data on the mammals with which various Utah species of black flies have been found associated.

Oviposition

The oviposition behaviour of a number of North American species of black flies has been reported by various authors. However, the egg-laying habits of many simuliid species remain unknown.

Published reports on the oviposition habits of *Prosimulium exigens* are lacking. The author observed oviposition flights of this species at Tryol Lake outlet, at an elevation of 10,050 feet, first on July 6 and again on September 11, 1956. On both occasions a small number of females of *P. exigens* were flying in association with large numbers of females of *Simulium arcticum*. The females of *Prosimulium exigens* oviposited by dipping their abdomens to the water surface as they were flying upstream. This has been observed by Davies and Peterson (1956) to be the usual method of oviposition for other species of *Prosimulium*.

The oviposition habits of *Eusimulium bicornis* (Dorogostajskij, Rubtzov and Vlasenko) are unknown to the writer, but many gravid females and two males of this species were collected on July 2, 1957, at Parley's Canyon Summit, Salt Lake County, at an elevation of 7,000 feet. These flies had been attracted to neon lights about one mile from their breeding place. A few females were collected as they flew about the head of the author.

Gravid females of *Eusimulium canonicolum* were collected in Utah as early as June 18, 1958, and as late as September 11, in 1956. On July 2, 1957, at Parley's Canyon Summit, large numbers of females and a few males were observed flying around neon lights at dusk. Many females were gravid while others

TABLE I
A summary of the mammals which different species of black flies have been found feeding on, or associated with, in Utah

Species	Mammals	Authority
P. exigens	Human*	Author.
P. flaviantennus	Human*	Peterson, 1958.
	Sheep*	Peterson, 1958.
	Cattle*	Peterson, 1958.
C. mutata	Human	Rees & Peterson, 1953; Peterson, 1956.
E. bicornis	Human*	Author.
E. canonicolum	Human	Author.
S. arcticum	Human	Rees & Peterson, 1953; Peterson, 1956; Author.
	Horse	Knowlton & Maddock, 1944; Author.
	Cattle	Author.
	Dog	Author.
S. bivittatum	Horse	Knowlton, 1935.
	Cattle	Knowlton, 1935.
	Pig*	Knowlton, 1935.
S. defoliarti	Human*	Stone & Peterson, 1958.
S. hunteri	Human	Rees & Peterson, 1953; Peterson, 1956; Author.
S. mediovittatum?	Horse*	Stains & Knowlton, 1943.
S. trivittatum	Human*	Author.
S. tuberosum	Human	Rees & Peterson, 1953; Peterson, 1956; Author.
	Golden-mantled ground squirrel	Peterson, 1956.
	Uinta ground squirrel	Peterson, 1956.
S. venator?	Horse*	Twinn, 1938.
S. venustum	Uinta ground squirrel	Author.
S. vittatum	Human	Peterson, 1956.
	Horse	Knowlton & Rowe, 1934a, 1934b; Knowlton, 1935; Twinn, 1938*; Knowlton & Maddock, 1944; Rees & Peterson, 1953; Peterson, 1956.
	Mule	Knowlton & Rowe, 1934a.
	Cattle	Knowlton, 1935; Peterson, 1956.
	Pig*	Knowlton, 1935.

*Flying about or landing but not feeding.

had recently oviposited as evidenced by the fact that only a few mature eggs remained in the abdomen. On September 11, 1956, at the headwaters of the Provo River, a few gravid females of *E. canonicolum* were collected ovipositing with females of *Simulium arcticum*, *S. jacumbae* and *Prosimulium exigens*. All of these species deposited their eggs by dipping their abdomens to the water's surface while in flight.

Ovipositing swarms of *Simulium arcticum* have been observed a number of times in Utah. On July 6 and September 11, 1956, and September 1, 1957, oviposition swarms were observed over the headwaters of the Provo River just below Tryol Lake. At 10:00 a.m. on July 6, females were flying from six inches to about 36 inches above the water surface, and were most numerous in shaded areas and places where the sun filtered through in spots between the trees. The

flies flew in small, but rather compact, groups of about 50 to 100 flies. Each group flew upstream, hovering and darting in a zig-zag manner. After flying in this manner for a short distance, they would return downstream to the original grouping position. The flies would dart to the water surface almost simultaneously, dip their abdomens to it, then climb steeply into the air and reform into a group. This same type of behaviour was noted for the other groups of *S. arcticum* females. On September 11, 1956, at 2:30 p.m., with an air temperature of 75° F. and a water temperature of 60° F., thousands of flies were observed in oviposition and mating flights. Ovipositing females were flying close to the water surface while mating males and females were flying three to four feet higher. The ovipositing females were separated into somewhat discrete groups that were dissipated and reformed in the manner noted above. Cross-stream flights were unusual and only rarely did any female dip to the water surface on a downstream flight. The eggs were deposited in most cases over a rocky bottom in the smoother water between ripples. Some dropped their eggs into the ripples. Similar observations were recorded for *S. arcticum* on September 1, 1957. On none of these three occasions were any females observed to lay their eggs on objects while not in flight. However, Peterson (1956) did observe females of this species laying their eggs while landed. Cameron (1922) observed the oviposition habits of *S. arcticum* (as *S. simile* Malloch) and stated that, "The eggs are not laid singly but in large cake-like masses, . . ." Fredeen *et al.* (1951) found that the eggs were apparently laid singly over the water and settled in the sand on the bottom of the stream. Thus, *S. arcticum,* like certain other black-fly species, has two distinct methods of oviposition, viz., by dropping eggs into the water while in flight and by depositing the eggs on some suitable surface while landed.

To the writer's knowledge, nothing has been reported previous to this study on the oviposition habits of *Simulium canadense* Hearle. On May 26, 1956, at the mouth of City Creek Canyon, near Salt Lake City, the author watched a small swarm of ovipositing females of *S. canadense*. At 4:00 p.m., two hours after a heavy rainstorm of short duration, a small swarm of six to 10 flies was noticed hovering and darting in a small, tight circle four to 12 inches from the downstream face of a large rock. A thin sheet of water was flowing at about two feet per second over most of the rock surface. The exposed portion of the rock was kept moist by a fine spray from the splashing water. One or two flies at a time would leave the swarm suddenly and land on the rock. Some landed where the rock was moistened by spray. The flies remained just long enough to touch the tips of their abdomens to the rock and deposit a single egg. They then quickly took to the air and climbed nearly straight up before drifting back downstream to rejoin the swarm. This procedure occurred repeatedly. When the flies took flight, the position of each egg on the rock could be seen clearly. The eggs were deposited with no apparent pattern, and formed a loose, irregular mass. Other females of *S. canadense* were observed to fly repeatedly into the spray, hitting the thin sheet of water with their abdomens and then climbing steeply into the air. Some flies were noted laying their eggs over the smooth water in the centre of the stream. About 10 feet upstream from the rock there was a three-foot high waterfall. A number of flies were flying about six to eight inches below the lip of the fall. These were observed to dart into the sheet of water flowing over the fall and then to climb steeply into the air. Many females were caught in the water and washed downstream; however, several were observed to come out of the water onto a rock and almost im-

TABLE II

The dimensions of gravid abdomens and number of eggs per female, and dimensions of mature eggs of nine species of black flies.

Species	Max. size of female abdomen in mm.		No. of eggs/female (No. of females)		Size of eggs in mm. (Av. and range are of 10 or more eggs in one or more females)						Authority
					Length		Width		Depth		
	Length	Width	Average	Maximum	Average	Range	Average	Range	Average	Range	
P. exigens	2.50	1.45	262 (2)	336	0.38	0.36–0.40	0.16	0.14–0.19	0.14	0.13–0.15	Author
P. flavivantennus	2.60	1.25	205 (1)	205	0.37	0.35–0.38	0.16	0.15–0.17	0.15	0.12–0.16	Author
E. bicornis	2.25	1.45	349 (3)	375	0.24	0.23–0.27	0.17	0.16–0.18	0.15	0.11–0.18	Author
E. canonicolum	1.75	1.25	426 (1)	426	0.24	0.23–0.26	0.16	0.15–0.18	0.13	0.10–0.15	Author
S. arcticum	2.00	1.25	135 (5)	162	0.28	0.26–0.32	0.18	0.16–0.23	0.15	0.13–0.17	Author
S. arcticum	–	–	–	–	0.33	–	0.24	–	–	–	Cameron, 1922
S. bivittatum	1.25	0.85	191 (1)	191	0.19	0.18–0.20	0.11	0.11–0.12	0.10	0.09–0.11	Author
S. canadense	2.35	1.30	282 (5)	336	0.28	0.24–0.32	0.16	0.13–0.21	0.14	0.11–0.16	Author
S. jacumbae	1.80	0.95	130 (1)	130	0.23	0.20–0.27	0.19	0.18–0.19	0.15	0.13–0.16	Author
S. tuberosum	1.75	0.85	225 (1)	225	0.21	0.20–0.23	0.11	0.10–0.13	0.09	0.09–0.11	Author
S. tuberosum	1.62	0.96	202 (4)	264	0.21	–	0.12	–	0.11	–	Davies & Peterson, 1956

mediately take flight. While the sun was shining the flies appeared to form several small groups but after the sun went down, these groups coalesced to form one large swarm. During this period of oviposition, a moderate wind was blowing, but the stream bed was protected by three- to four-foot banks on either side and was covered by a rather dense stand of chokecherry trees (*Prunus virginiana* var *melanocarpa*). The air temperature dropped from 73° to 68° F. during the period of observation until darkness terminated the study.

Davies and Peterson (1956) were able to demonstrate that a light pressure applied to the ventral surface of the gravid female abdomen would cause the eggs to be extruded one by one. This pressure applied to a relatively small area may be responsible for the extrusion of individual eggs. This is evidenced by the fact that the females of *Simulium canadense* as they hit a solid surface often do so with the tip of the abdomen and release a single egg with each tap. However, more than one egg can be released at a time and this may result from a more flattened approach to the surface which would result in a stroking pressure along the abdomen forcing several eggs out at a time. The eggs of *S. canadense* emerge from the abdomen blunt end first.

Variations in the Number, Size, and Shape of Eggs

The number of eggs per female varied in the different species and among females of the same species. Most gravid females examined were netted from oviposition swarms and undoubtedly most of them had already deposited a number of eggs. For this reason, the maximum number of eggs indicated in Table II may be somewhat lower than the number that actually exists in nature.

The size and shape of mature eggs also varied in the different species, but little variation was noted within a species. The eggs of *Simulium canadense*, *S. jacumbae* and *S. arcticum*, in that order, showed the greatest variation in length, and the eggs of *S. canadense* and *S. arcticum* showed the greatest variation in width. *Eusimulium bicornis* showed the most variation in depth of the eggs. The eggs of *Prosimulium* are larger and tend to be narrower in relation to length than those of *Eusimulium* and *Simulium* as was found also for Ontario species by Davies and Peterson (1956). The eggs of *S. bivittatum* resemble *Prosimulium* eggs, while those of *S. jacumbae* appear somewhat spherical as opposed to the more triangular form found among the other species of *Simulium*. Table II presents a comparison of these features for nine species collected in Utah.

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Note on Occurrence in British Columbia of the Omnivorous Leaf Tier, *Cnephasia longana* (Haw.) (Lepidoptera: Tortricidae), as a Pest of Strawberry[1]

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The senior author collected several nearly mature lepidopterous larvae found tunnelling in ripening strawberries at Saanich, Vancouver Island, B.C., on June 10, 1957. From larvae reared on fruit in cages in an insectary, six moths emerged, two each on July 15, 18, and 22. These six and another individual collected in flight were identified as the omnivorous leaf tier, *Cnephasia longana* (Haw.).

Samples of wormy strawberries were received by the junior author on June 10, 1957, from a processing plant at Clearbrook, B.C., in the lower Fraser Valley. The fruit originated from two plantings in the Abbotsford-Clearbrook area. Four lepidopterous larvae were removed from the samples; one specimen was preserved immediately and an unsuccessful attempt was made to rear the remainder. The larva was identified as *C. longana*.

Infestations of the insect were discovered during 1958 in three widely separated strawberry plantings in Saanich. Larvae were collected from both strawberry fruit and foliage, and also from thistle, vetch, and clover in pasture areas near the infested strawberry plantings.

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Infestations of the insect also occurred during 1958 throughout most of the major strawberry-growing areas in the lower Fraser Valley. Larvae were collected from strawberries at Yarrow, Abbotsford, Clearbrook, and Cloverdale, and also from Canada thistle in the Clearbrook area.

Few infestations of this insect were reported in the lower Fraser Valley from strawberry plantings that received spring applications of malathion or Diazinon for aphid control.

This European insect is a serious pest of strawberry, flax, vetch, and a wide range of other plants in California, Oregon, and Washington (Pritchard *et al.*, 1949; Rosenstiel *et al.*, 1944; Stitt and Allmendinger, 1953). According to Dr. T. N. Freeman (in litt.), this pest has not been reported in Canada previously. It was first recorded in Oregon in 1929 by Edwards and Mote (1936), who described the life-history. Rosenstiel *et al.* (1944) reported on the oviposition habits of the moth, which lays eggs only on rough surfaces such as the bark of trees or fence posts. In the early spring, larvae are carried by the wind to host plants. Young larvae mine the leaves and later tie them together. As they approach maturity, the larvae enter ripening strawberries beneath the calyx caps. One larva usually damages several berries. Satisfactory control was obtained with parathion, DDD, or DDT sprays on ornamentals in California (Pritchard *et al.*, 1949) and with methoxychlor dust on strawberries and nursery stock in Oregon (Rosenstiel, 1953).

A single parasite, identified as *Atrometus* sp., was reared from larvae collected at Saanich.

Larvae were identified by Miss Margaret Rae MacKay, adults were determined by Dr. T. N. Freeman and Dr. D. F. Hardwick, and the parasite was identified by Mr. C. D. Miller, Insect Systematics and Biological Control Unit, Entomology Division, Ottawa.

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A New Species of *Anoplodera* Mulsant in the *mutabilis-aspera* Group (Coleoptera: Cerambycidae)[1]

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In the genus *Anoplodera* two species, *mutabilis* Newman and *aspera* LeConte, represent a small, distinct group. A third species, previously unrecognized and closely related to *aspera*, has been noted in material submitted for identification. The present description and distributional notes are based on material in the California Academy of Sciences, the Canadian National Collection, Cornell University, Ohio State University, the United States National Museum, and the personal collections of Dr. J. N. Knull, Ohio State University, Columbus, Ohio, and Mr. C. A. Frost, Framingham, Mass. I wish to thank Dr. Knull for examining some of the eastern specimens that have been confused with *aspera;* he concurred that they represented an undescribed species.

According to Swaine and Hopping (1928, p. 57) the *Anoplodera mutabilis-aspera* group can be distinguished by: "the quadrate pronotum, open forecoxal cavities, and the pubescent sole on the first segment of the hind tarsi" (the latter true only of *mutabilis*). These authors included these two species in *Anoplodera* because of the convex pronotum and "other characters". In their introduction (p. 9) they stated that Dr. Craighead found the larvae of *aspera* and *mutabilis* to represent a rather isolated group in the genus. They seem to have overlooked the fact that Casey (1913, p. 271) proposed the subgenus *Trachysida* in *Anoplodera* with *mutabilis* as the type of the subgenus. However, in their key to species in the genus *Anoplodera*, Swaine and Hopping (1928, p. 41) indicated that *aspera* and *mutabilis* could be included in the genus *Nivellia* Mulsant (1863, p. 564). For the present, I have deemed it best to continue the usage of the generic name *Anoplodera* for the species considered here.

The species of the *mutabilis-aspera* group can be separated by the following key:

1. Surface between elytral punctures smooth and shining; second segment of hind tarsus, third, and portion of first with pubescent soles; terminal segment of antenna of male with carinate line ..... *mutabilis* (Newm.)
   Surface between elytral punctures granulate and dull; third segment of hind tarsus with pubescent sole, second segment often with indication of sole; terminal segment of antenna of male lacking carinate line 2
2. Punctures in basal half of elytra mostly separated by a distance equal to one diameter or more; front of head, measured from ridges above antennal insertion to anterior margin of clypeus, elongate, nearly as long as width of head below eyes. Western Canada and western United States ..... *aspera* (Lec.)
   Punctures in basal half of elytra mostly separated by a distance equal to less than one diameter; front of head, measured from ridges above antennal insertions to anterior margin of clypeus, noticeably shorter than in *aspera*, similar to that of *mutabilis*. Eastern Canada and northeastern United States ..... *brevifrons* n. sp.

Anoplodera mutabilis (Newman)

Leptura mutabilis Newman, 1841, p. 71. Lectotype here designated: ♀, labelled "mutabilis Newn. Entomol. 1-71. Trenton Falls, U.S." and "Ent. Club. 44-12" and also with British Museum (N.H.) type label (fide W. J. Brown, 1958).
Stenura luridipennis Haldeman, 1847, p. 63.
Leptura quadricollis LeConte, 1850, p. 339.
Leptura laetifia Provancher, 1877, p. 620.
Leptura provancheri Aurivillius, 1912, p. 223.

This species, though varying from brown to black and ranging from nine

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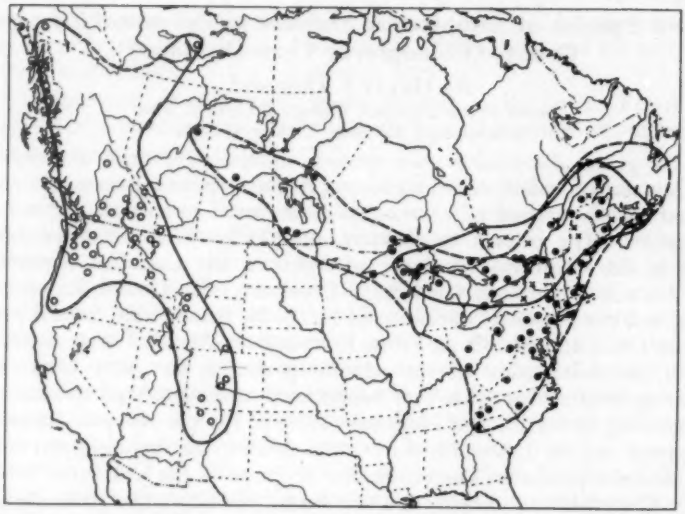

Distribution of *Anoplodera mutabilis* (Newman [●], *Anoplodera aspera* (LeConte) [O], and *Anoplodera brevifrons* new species [X].

to 18 mm. in size, can easily be separated from the two closely related species by the characters given in the key. The range of the species, as indicated in the map, is from Alberta eastward in Canada, and in the eastern United States southward to northern Georgia. Host records for the species include dead trees of a number of hardwood genera: *Quercus, Betula, Acer, Castanea, Carpinus, Almus,* and *Populus.*

Anoplodera aspera (LeConte)

Leptura aspera LeConte, 1873, p. 228.
Leptura aspera var. *parkeri* Hippisley, 1922, p. 66.

Anoplodera aspera is a western species, described from Vancouver Island, ranging from the Yukon Territory southward into New Mexico. The majority of specimens are entirely black and slightly larger in size than the related eastern species described here. To a reddish form that has been occasionally collected in British Columbia the varietal name *parkeri* Hippisley has been applied. The few specimens seen from Colorado and New Mexico can be distinguished from more northern populations by the long, yellowish elytral setae. However, the clinal area in which the setae become shorter and nearly black apparently shows no abrupt region of change. Because of this wide zone of intergradation, it does not seem wise to assign the southern population subspecific status, at least until more material becomes available. Swaine and Hopping (1928, p. 57) listed *Betula* sp. as the host. In addition, I have examined specimens labelled as reared from "*Pinus contorta*" and "Engelmann spruce".

Anoplodera brevifrons new species

Holotype.—Male, length 9.8 mm., greatest width 2.7 mm. Head, thorax and abdomen black; legs, elytra, and last seven segments of antenna brownish-black, appearing a dull black when examined macroscopically.

Labrum arcuate, more strongly so laterally than anteriorly; setate-punctate laterally. Clypeus truncate and smooth anteriorly, becoming strongly setate-punctate and declivous posteriorly. Frons densely setate-punctate with a deep median sulcus between antennal ridges. Front of head, measured from top of

antennal ridges to anterior margin of clypeus, about four-fifths as long as width of head below eyes, distinctly shorter than front of *aspera*. Vertex heavily, confluently punctate; most punctures bearing a short, yellowish seta. Antenna extending at least one full segment beyond elytral apex; first four segments and base of fifth shining, the remaining segments dull, finely and closely setate-punctate. First antennal segment (scape) stocky; second nearly oval; third elongate, about three-fourths as long as first. Fourth five-sixths as long as third; remaining segments all slender and elongate, from 1½ to over twice as long as the basal segment.

Pronotum as long as wide, widest basally; anterior constriction shallow, basal constriction only faintly indicated; sides of pronotum nearly straight; lateral swelling before basal constriction vague, not nearly as pronounced as in *aspera*. Pronotal surface coarsely, contiguously punctate; each puncture with a small, recurved, yellowish seta.

Scutellum triangular, confluently punctate; each puncture bearing a short, recurved seta. Elytra widest basally, sides sinuate; apex of each elytron rounded in outer half, briefly truncate near suture. Elytral disc coarsely, heavily punctate, more so basally than apically. Basal punctures mostly separated by a distance of less than one diameter; apical punctures separated by a distance of one to two diameters. Each puncture with a distinct shining tubercle at its anterior margin and with a short, yellowish, recurved seta arising from its center. Surface between punctures granulate and dully shining, the granules larger than those of *aspera*. Setae at apex of elytron yellowish and more widely separated than those of *aspera*. Ventral flattened portion of head behind mouth parts as in *aspera*, but not quite as elongate. Prosternum distinctly impressed behind anterior margin; lateral median portions of prosternum not noticeably swollen as is usual in *aspera*. Thoracic sterna rugose and setate-punctate except for median line of metasternum, which is impressed and impunctate. Abdominal sternites rugose and setate-punctate; posterior sternites slightly flattened near their apices. Last abdominal tergite with posterior margin shallowly emarginate. Legs similar to those of *aspera*. First three tarsal segments of first two pairs of legs with pubescent soles, hind leg with only third tarsal segment with a definite pubescent sole, as in *aspera*. Only *mutabilis* has the second and third tarsi of hind leg with definitely pubescent soles, and a partial sole on first segment.

Allotype.—Female, length 10 mm., greatest width 3.3 mm. Similar to holotype except in following respects: body stouter; front of head more elongate; thorax wider than long; sides of elytra less sinuate; antennal segments six to eleven attenuate, not extending to elytral apices; and abdomen swollen, with last segment more elongate than in males and lacking the emargination.

Type Material.—Holotype, male, Mt. Lyall [Gaspé Peninsula], Que., 1500 ft., July 4, 1933, W. J. Brown [CNC No. 6776]. Allotype, female, Forestville, Que., July 7, 1950, R. de Ruette [CNC No. 6776].

Paratypes, 30 ♂♂, 16 ♀♀. CANADA:—*New Brunswick*: 4 ♂♂, Bathurst, June 20, 1922, J. N. Knull; 1 ♂, Fredericton, July 2, 1928, W. J. Brown. *Nova Scotia*: 1 ♀, Halifax, 1900; 1 ♀, Millsville, 1908; 1 ♀, New Ross, July 7, 1952, V. R. Vickery. *Ontario*: 1 ♀, Mer Bleue [Ottawa], May 31, 1898. *Quebec*: 1 ♂, 1 ♀, Duparquet, July 16, 1936, G. Stace Smith, on yarrow; 1 ♀, Forestville, July 7, 1950, R. de Ruette; 2 ♂, Gaspé Co., July 8, 1933, July 27, 1934, E. B. Watson; 1 ♂, 1 ♀, L. Opasatika, June 5, 1922, J. N. Knull; 1 ♂, 2 ♀, Laniel, June 27, 1934, July 4 and 6; 11 ♂♂, 1 ♀, Mt. Lyall [Gaspé Peninsula], 1500 ft. July 4, 1933, W. J. Brown; 1 ♀, N. Dame des Laurentides, June 18, 1949, R. Lambert; 1 ♀, Portneuf, June 25, 1934, Bro. Anslem; 1 ♂, Wright,

May 26, 1933, W. J. Brown. UNITED STATES:—*Maine*: 1 ♂, Aziscoos Lake, [Oxford Co.], July 9, 1916, C. A. Frost, Umbelliferae flowers; 1 ♂, 1 ♀, Kineo, June. *Michigan*: 1 ♂, Detroit, Hubbard & Schwarz; 1 ♀, Eagle Harbor, L. Superior, June 9, Hubbard & Schwarz; 1 ♂, 2 ♀♀, Marquette, June 27, July 7 and 8, Hubbard & Schwarz; 1 ♀, Sault, L. Superior, July 21, Hubbard & Schwarz. *New York*: 1 ♂, Catskill Mts.; 1 ♀, Lake Colden, Essex Co., July 1, 1945, H. Dietrich; 1 ♂, McLean Bogs Reserve, Tompkins Co., June 5, 1953, J. G. Franclemont; 1 ♂, Top Mt. MacIntyre, July 29, 1940, H. Dietrich.

Paratypes are deposited in all of the collections from which material was borrowed.

Variation in the type series is most evident in size and color. Males range from 8.5 to 10 mm. in length and from 2.3 to 3.0 mm. in greatest width. Females range from 10 to 14 mm. in length and from 2.9 to 3.9 mm. in greatest width. Though the head, thorax and abdomen are black in all specimens examined, the elytra vary from nearly black to tan with the elytral apices often dark brownish-black. The shape of the thorax shows some variation, in some males being slightly wider than long. The elytral punctures vary in density, but seem more closely spaced than in *aspera*. Also the frons varies in length, being usually more elongate in females.

Many of the specimens of *brevifrons* were collected in areas commonly referred to as "cold bogs". One specimen was labelled "spruce" and two reared specimens emerged from a standing dead balsam snag.

In a comparison of a series of *brevifrons* with *aspera*, the eastern species, *brevifrons*, appears to average slightly smaller, with a much greater proportion of specimens having tan elytra; macroscopically *aspera* usually appears duller and more intensely black. The third antennal segment is shorter in *brevifrons* than in *aspera*, but this character shows some variation, as does the more strongly swollen pronotum of *aspera*. The most reliable characters for separating *brevifrons* from *aspera* or *mutabilis* are given in the key.

Summary

The *mutabilis-aspera* group of *Anoplodera* contains three species. The eastern species, which has been confused with *aspera*, is described under the name *Anoplodera brevifrons*. A key to the three species and a distributional map is included.

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Pyralidae from the Collection of the California Academy of Sciences (Lepidoptera)[1]

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Through the kindness of Mr. Hugh B. Leech I have been able to examine a large number of Pyralidae from the collection of the California Academy of Sciences, San Francisco. Five new species found in this material are described here. A new genus is described to accommodate two of the species, and two known species are transferred from the genus in which they were described.

PYRAUSTINAE

Desmia filicornis, new species

Figs. 1, 7

Antenna of male filiform, annulated with scales, dark fuscous; frons scarcely prominent, dark metallic green, with a narrow white line on each side and scattered white scales at lower margin; proboscis white-scaled at base; labial palpus black, under side of first joint and a fringe at end of second joint white; vertex dark fuscous with some pale-buff scales on occiput; thorax above and abdomen above and below dark fuscous, with dark, metallic, greenish-blue iridescence, strongest on patagium and tegula; thorax beneath and legs dark fuscous, a white stripe across prothorax and base of fore coxa, tarsal segments dusted with white, most strongly in basal portions, a white stripe before apex of mid-femur, a slightly weaker one on hind femur. Fore wing with costa nearly straight to near apex, outer margin strongly oblique, weakly excurved; upper surface dark fuscous, with weak, generalized, violaceous iridescence and rather strong greenish-blue iridescence somewhat irregularly distributed in the basal half. Hind wing short and triangular, apical and anal angles somewhat rounded; ground colour above dark fuscous, an oblique semitransparent median band, with strong greenish-blue iridescence and bearing a black discocellular bar. Under side like upper side, but with iridescence bluer and more generalized. Expanse 24-28 mm.

Male genitalia. Typical of the genus. Penis with a curved sclerite bearing a row of seven very stout spine-like cornuti, a single free spine just beyond the sclerite, then a well-separated group of two larger spines, followed immediately by a group of four, not quite so large.

Holotype, male, Potrerillos, Panama, June 4, 1935. J. W. MacSwain. Four male paratypes, same locality and collector, dates from May 26 to June 28, 1935. Holotype and two paratypes in California Academy of Sciences; two paratypes in Canadian National Collection, Type No. 6723.

Similar to *Desmia daedala* (Druce), new combination, and *D. hadriana* (Druce), new combination, both of which were described in *Acridura*, but which clearly belong in *Desmia* on genitalic characters. *Desmia filicornis* is distinguished from both of these species by the simple antenna of the male and by the semitransparent iridescent band of the hind wing. This group of mimetic species forms an interesting addition to the compact genus *Desmia*.

Mecyna cocosica, new species

Figs. 2, 8

Frons fulvous, suffused with brown; vertex light brown, with some light-buff scales; labial palpus brown, base white beneath, third joint fulvous above;

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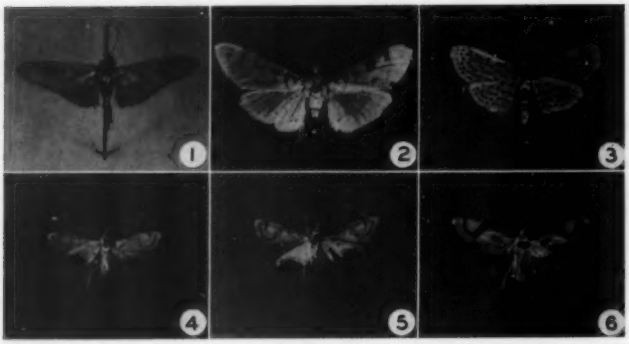


Figs. 1-6. 1, *Desmia filicornis;* ♂, 2, *Mecyna cocosica,* ♂; 3, *Polygrammodes naranja,* ♂; 4, *Callilitha boharti,* ♂; 5, *C. boharti,* ♀; 6, *C. tenaruensis,* ♂.

thorax above yellow anteriorly, white posteriorly, a dark-brown stripe in front of base of fore wing; abdomen above with terga brown anteriorly, yellow in middle and white posteriorly; body beneath white, tinged with yellow; legs light buff. Fore wing with outer margin oblique (probably less so in female); upper surface pale yellow, becoming whitish towards tornus; costa fulvous; an obscure, inwardly oblique, dark-brown, sub-basal line, obsolescent towards inner margin; an erect, weakly curved, dark-brown antemedial line, tapering behind; orbicular obscure, quadrate, dark brown, followed by a brown dot behind cell; reniform obtrapezoidal, fulvous, bordered inwardly, outwardly and posteriorly with dark brown; postmedial line obscure, dark brown, thick and weakly inwardly oblique from costa to M_1, offset outward on M_1, then slender and erect to Cu_2, there strongly offset inward, and weakly inwardly oblique to 2nd A; apical and marginal areas very faintly infuscated. Hind wing above white, a weak, dark, discocellular bar; a weak, fuscous, postmedial line, beginning at R_s, oblique and straight to Cu_2, then offset inward and more strongly oblique to inner margin; marginal area very faintly infuscated. Under side of fore wing white, tinged with yellowish on costal half, antemedial and postmedial lines and orbicular and reniform spots very faintly indicated in costal half of wing. Hind wing beneath uniformly white. Expanse 29 mm.

Male genitalia. Uncus more slender and spatulate than in typical members of the genus. Penis rather weakly sclerotized, with one long, slender, thorn-like cornutus and two shorter tooth-like ones. Valve and other structures normal for the genus.

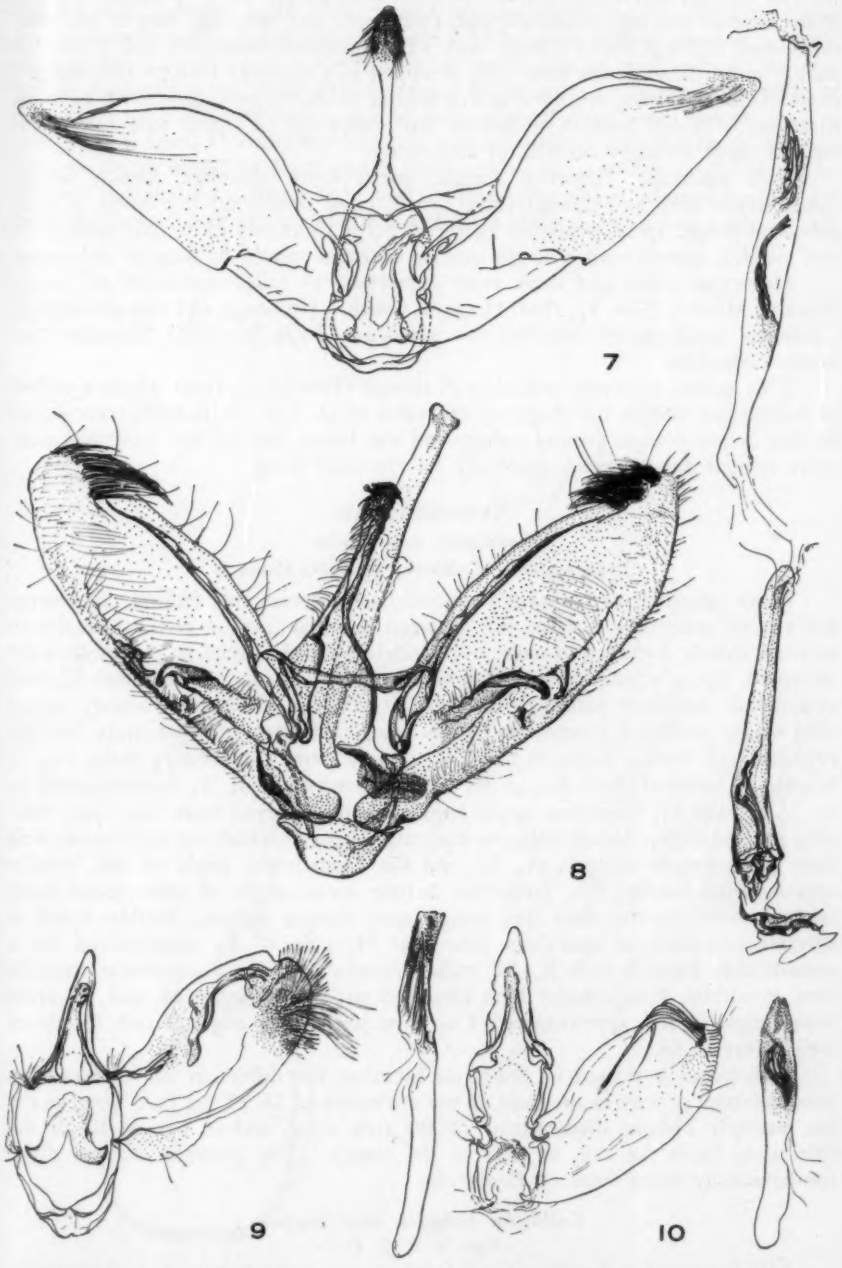
Holotype, male, Cocos I., Sept. 10, 1905, F. X. Williams, in the California Academy of Sciences.

This is one of the few Lepidoptera known from this island in the eastern Pacific. As is to be expected, the species is of Neotropical affinity. The dark markings are much reduced as compared with those of any American mainland species known to me.

Polygrammodes naranja, new species

Figs. 3, 12

Frons flat and oblique, orange, with a purplish-brown triangle at each antero-lateral angle; labial palpus purplish brown, white at base below, the white and dark areas separated by a yellowish-orange zone; vertex yellow, with erect scales; thorax and abdomen above orange; patagium purple; tegula with a pur-



Figs. 7-10. Male genitalia. 7, *Desmia filicornis;* 8, *Mecyna cocosica;* 9, *Callilitha bohartí;* 10, *C. tenaruensis.*

plish spot; each abdominal tergite with a pair of dorso-lateral purple spots at anterior margin and a single, transverse, median, purple bar at posterior margin. Body beneath and legs yellowish buff, fore femur and tibia and base of mid-tibia infuscated. Wings above orange, with a faint purplish sheen, and with numerous purple spots, those of the fore wing arranged in a complex pattern (see figure), those of the hind wing arranged in five oblique rows; fringe yellow, with a golden basal line. Wings beneath yellowish buff, markings of upper side faintly indicated, most strongly on disc of fore wing.

Male genitalia. Tegumen domed; uncus short, spatulate, weakly setose; subscaphium long and strong; valve broad, costa somewhat thickened, a weak subcostal flange, apices probably ligatured, harpe short and decurved; penis short and slender, armed with a single slender cornutus nearly as long as aedoeagus.

Holotype, male, and three male paratypes, 17 miles northwest of Tepic, Nayarit, Mexico, Nov. 12, 1948, Hugh B. Leech. Holotype and one paratype in California Academy of Sciences; two paratypes, Type No. 6722, Canadian National Collection.

This species is closely related to *P. elevata* (Fabricius), from which it differs in maculation and in the shape of the valve (Fig. 11). It is easily recognized by the bright-orange ground colour and the larger size of the spots and their more regular arrangement, especially on the hind wing.

NYMPHULINAE

Callilitha, new genus

Type species: *Callilitha boharti* Munroe

Frons rounded, vertex mostly smooth, a transverse tuft behind chaetosema and a small, anteriorly directed tuft between antennae; ocellus vestigial or absent; antenna weakly flattened in male, cylindrical in female; labial palpus moderately upturned, not reaching vertex; first and second joints moderately scaled, third cylindrical; maxillary palpus prominent, moniliform, third joint weakly tufted with scales; proboscis prominent. Fore wing moderately narrow, outer margin rounded, cell with a fovea in male; R_1 free or briefly stalked in male, free in female; R_2 stalked with R_{3+4}; R_3 and R_4 long-stalked; R_5 approximated to R_{3+4} at base; M_1 from near upper angle of cell, decurved from base, then running parallel to R_5; discocellular very strongly bent at middle of cell; lower limb long and strongly oblique; M_2, M_3 and Cu_1 from lower angle of cell, weakly approximated basally; Cu_2 from just before lower angle of cell. Hind wing fairly narrow, shorter than fore wing, outer margin oblique, weakly lobed at anterior boundary of speculum (about at M_2); $Sc + R_1$ anastomosed for a considerable distance with R_s; M_1 stalked briefly with R_s; discocellular strongly bent at middle of cell, lower limb long and strongly oblique; M_2 and M_3 from lower angle of cell, approximated; Cu_1 from just before angle of cell, Cu_2 from well before angle.

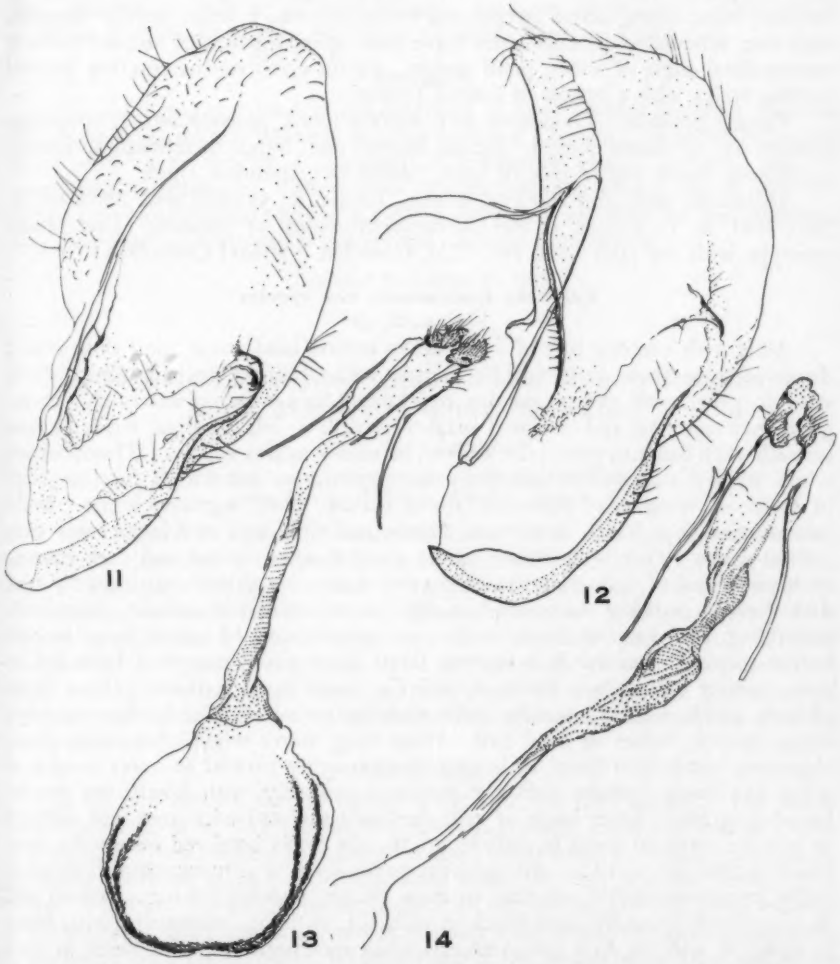
This genus is related to *Eoophyla* Swinhoe but differs in the absence of a basal antennal process in the male, in the curvature of M_1 of the fore wing, in the less strongly oblique discocellular of the fore wing, and in having R_1 of the fore wing from the cell, at least in the female. The genitalia do not differ fundamentally from those of *Eoophyla*.

Callilitha boharti, new species

Figs. 4, 5, 9, 13

Mid-femur of male dilated and with a prominent brush of dark, hair-like scales, mid-tibia somewhat thickened; hind tibia thickened, abruptly tapering

and somewhat bent distally. Female without these specializations. Head, thorax, and abdomen above white; patagium, tegula and distal part of abdomen marked with fulvous; body beneath and legs mainly white. Fore wing above white, costa broadly violaceous to before middle, then yellow to apex; a weak, oblique, black fascia from inner margin at one-fourth to anal fold; an oblique, yellow, outwardly obscurely dark-bordered fascia from costa beyond middle to tornus; a broad, dark-bordered, yellow fascia curved from costa before apex to meet oblique fascia at lower angle of cell; a broad, yellow, terminal fascia, bordered inwardly by a row of black dashes from vein to vein and outwardly by a row of black terminal dots; fringe light buff. Hind wing above white, a small black fascia across anal area before middle; an obscure black dot at lower angle of cell;



Figs. 11-14. Genitalia. 11, *Polygrammodes elevata*, ♂; right valve; 12, *P. naranja*, ♂, right valve; 13, *Callilitha bobarti*, ♀; 14, *C. tenaruensis*, ♀.

an incurved, black, postmedial fascia, followed by an area powdered with black and a few bluish-grey scales; just before apex a small oblique area of concentrated blue-grey scales with silvery reflections; a diffuse, black, subterminal fascia following the powdery area and bearing four silvery crescents or triangles in an oblique series in cells M_1 to Cu_2; an orange apical fascia, separated by a grey area with coppery reflections and by a black area from the orange terminal fascia; the latter extending from behind M_1 to before anal fold, and bearing four large round black spots, one opposite each silvery crescent; the terminal fascia followed by a powdery grey area. Fore wing beneath white, the markings of the upper side faintly indicated. Hind wing beneath white, with four black spots on termen. Expanse 17-19 mm.

Male genitalia. Uncus narrowly triangular, its apex acute; gnathos finger-like, somewhat decurved, with a few dorsal spines; tegumen and vinculum narrow; valve ovate, distal margin somewhat sinuous; a large, basally directed, club-like, articulated process from valve near apex; a patch of slender setae at ventro-distal angle of valve; penis slender, ductus ejaculatorius entering beyond middle, vesica with a bundle of barbed cornuti.

Female genitalia. Ovipositor soft, weakly lobed, sparsely setose; apophyses slender, of moderate length; ductus bursae and bursa membranous, weakly scobinated, bursa with a pair of long, ribbon-like, spinulose signa.

Holotype, male, and allotype, female, Tenaru R., Guadalcanal, Solomon Is., Jan., 1945, R. E. Bohart, in the California Academy of Sciences. One female paratype with the same data, No. 6720, Canadian National Collection.

Callilitha tenaruensis, new species

Figs. 6, 10, 14

Male with a strong tuft of white scales behind hind coxae, hind tibia with a decurved zone about at its middle; female without these specializations. Frons smooth, grey, with yellow median and lateral lines meeting anteriorly; vertex grey, inter-antennal and occipital scale-tufts yellow; labial palpus white at base beneath, then fuscous, third joint yellow; maxillary palpus yellow. Thorax above white, stained with yellow anteriorly and posteriorly, and with a fuscous stripe in front of wing-base; abdomen above yellow, basal segment white. Body beneath and legs white, fore coxa, femur and tibia and mid-femur and tibia yellow above. Fore wing above white; a costal stripe, broad and dark fuscous to beyond end of cell, then narrowing and becoming yellow; an oblique, oval, dark-fuscous marking above inner margin at one-third; an oblique, posteriorly narrowing, dark-fuscous fascia from costa opposite end of cell to inner margin before tornus; a curved dark-fuscous fascia from costal margin a little before apex, joining the oblique fascia in cells Cu_1 and Cu_2; a terminal yellow fascia of even width, defined inwardly and outwardly by a black line broken on veins; fringe brown, darker in basal half. Hind wing above white; postmedial fascia beginning just behind costa, its inner margin roughly parallel to outer margin of wing, the fascia yellow, diffusely bordered inwardly with black, the border broadest opposite lower angle of cell, the fascia suffused with grey and diffused to join the terminal fascia in cells M_1 to M_3, the fascia bordered outwardly with black in cells Cu_1 and Cu_2, uniting with terminal fascia at inner margin; terminal fascia orange anteriorly, shading to deep yellow posteriorly, narrowest in cell M_1, bordered inwardly with black in cells Cu_1 and Cu_2, outwardly with black in cells Cu_2 and 1st A; a round silvery-white spot bordered with black in each of cells M_2, M_3 and Cu_1, each spot followed by a quadrate black terminal patch; a narrow grey apical shade; fringe grey, with a darker line near base. Wings

beneath white, with markings of upper side faintly visible; hind wing with prominent black marginal spots in cells M_2, M_3 and Cu_1, each preceded by a white crescent, and that in cell Cu_1 preceded by a black line. Expanse 21-24 mm.

Male genitalia. Uncus subtriangular, outer margins weakly convex, apex narrowly rounded; gnathos finger-like, finely spinulose dorsally; tegumen and vinculum narrow; juxta large, weakly sclerotized; valve ovate, subangulate at tip, inner surface weakly striated, a patch of about half-a-dozen strong, apposed, bent setae before apex; penis cylindrical; ductus ejaculatorius entering before middle; distal part of penis finely scobinated; vesica with a short curved cornutus.

Female genitalia. Ovipositor weakly lobed, very weakly setose; apophyses slender and weakly sclerotized; ductus bursae short, bursa long and slender, rather strongly spinulose in basal part.

Holotype, male, and allotype, female, Tenaru R., Guadalcanal, Solomon Is., Jan., 1945, R. E. Bohart, in the California Academy of Sciences. One female paratype with the same data, No. 6721, Canadian National Collection.

Summary

The following pyralid taxa are described as new: *Desmia filicornis*, Panama; *Polygrammodes naranja*, Mexico; *Mecyna cocosica*, Cocos Is.; *Callilitha*, Nymphulinae, with new species *C. boharti*, Guadalcanal (type species), and *C. tenaruensis*, Guadalcanal. The species *Acridura daedala* Druce and *A. hadriana* Druce are transferred to the genus *Desmia*, of which, together with *D. filicornis*, they comprise a previously unrecognized mimetic component.

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The *Pegomyia hyoscyami* (Spinach Leaf Miner) Complex in North America (Diptera: Muscidae)[1]

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The "spinach leaf miner" – referred to in North American literature consistently as *Pegomyia hyoscyami* (Panzer) or, in early years, as *P. vicina* Lintner and in European literature under a variety of names (*hyoscyami*, *atriplicis* Goureau, *chenopodii* Rondani, *betae* Curtis, *spinaciae* Holmgren, etc.) – is known to represent a complex in Europe of at least two species, with different morphology and host preferences. The present paper records the presence of these two species in North America, points out the recognition characters of the Nearctic forms, and summarizes the known ecological and outbreak data for the species in Canada.

Life-History

So far as is known, the life-history is the same for both species. The larvae mine the leaves of spinach (*Spinacia oleracea* L.); beets, sugar beets, swiss chard, and mangels (*Beta vulgaris* L.); *Dianthus* sp.; *Datura metel* L.; and several weeds, including *Arctium lappa* L., *Chenopodium album* L., and *Atriplex hastata* (L.) Gray. Eggs are laid on the under surfaces of the leaves, and the larvae burrow into the leaves upon hatching, feed in the soft cells of the mesophyll, and form large, communal, blotch mines. The mature larvae usually drop from the leaves

[1]Contribution No. 3890, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

and pupate in the soil. There are normally several generations per year. Cameron (1914) gave a detailed account of life-history and ecology in England, with several excellent illustrations, and Frost (1923) gave a similar account of the species in North America.

The Species Complex in Europe

In Europe, several specific and varietal names have been used for forms closely related to *hyoscyami* but differing somewhat in color and host preferences. Workers now recognize two distinct species (or subspecies), *P. hyoscyami* and *P. betae*, the first common on a wide variety of plants of Chenopodiaceae and Solanaceae and the second common on, and apparently restricted to, Chenopodiaceae. D'Aquilar and Missonier (1957) listed several morphological differences between *hyoscyami* and *betae* and considered them as distinct species, a conclusion with which I fully agree. Whether still further species are present in the *hyoscyami* complex in Europe is a question that must be left for further study. I consider it very likely, as specimens from Czechoslovakia that I examined appear externally to be identical with *hyoscyami* but have a distinctly more elongate male surstylus.

D'Aguilar and Missonnier separated *betae* and *hyoscyami* on the structure of both male and female genitalia; on the width of the parafacials and frontal vitta in the male; and on color. The dark species ("forme foncée"), *betae*, has the basal antennal segments, palpi, and femora largely infuscated, and the female abdomen uniformly grey; whereas *hyoscyami* ("forme claire") has these structures largely pale or reddish and the female abdomen marked with brown. They also found that *betae* showed a very distinct preference for *B. vulgaris* during oviposition, and could be reared successfully only on that plant, whereas *hyoscyami* oviposited with equal readiness on species of *Beta*, *Chenopodium*, and *Datura* (*Solanaceae*) and could be reared successfully on all three.

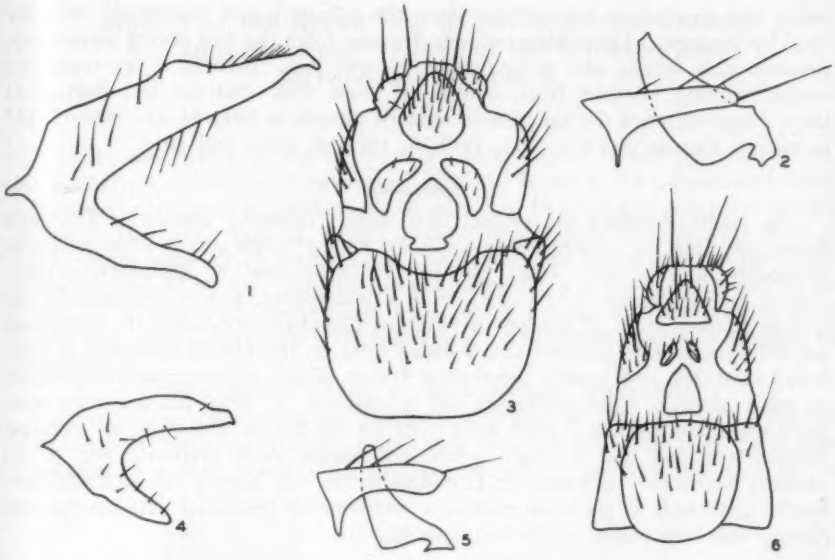
The Species Complex in North America

H. C. Huckett (1941) was unable to recognize any colour differences such as were recorded for European varieties, and treated all Nearctic specimens as of *hyoscyami*.

However, as recent European research indicated correlated structural characters, I reexamined Nearctic material of this complex. No color variants, such as are obvious in Europe, can be found in Nearctic material, but the distinct structural differences that separate *betae* and *hyoscyami* are present. Externally, the only characters to separate them are the almost contiguous male parafrontals in *hyoscyami* (distinctly separated by a broad frontal vitta in *betae*), and a brown median vitta on the female abdomen of *hyoscyami* (very faint or absent in *betae*). There is also an average difference in size, *betae* being the larger. Internally, the genitalic characters of both male and female clearly separate the two species, and indicate their identities with the European species.

The male surstyli, as figured by d'Aguilar and Missonier, differ strikingly in the two species. In *hyoscyami* (Fig. 1), the surstylus is very short and only weakly haired, the upper limb broad with a wide dorsal flange, the lower limb moderately broad. In *betae* (Fig. 2), it is elongate and strongly haired, the upper limb slender with an apical hook and a median dorsal hump, the lower limb also slender. The aedeagus (Figs. 3, 4), in addition, is more strongly modified at the apex in *betae*, and the pregonite is more elongate and slender.

The female ovipositors also show reliable differences. In *hyoscyami* (Fig. 5), the eighth sternite is weakly sclerotized and only indistinctly divided into



Figs. 1-3. *Pegomyia betae*. Figs. 4-6. *P. hyoscyami*. 1, 4, Surstyli, lateral views. 2, 5, Pregonites and aedeagi, lateral views. 3, 6, Ovipositors, ventral views.

median and lateral plates, whereas in *betae* it is strongly sclerotized with distinct median and lateral plates, as well as a strong but indistinctly separated basal plate.

In North America, *P. hyoscyami* has been reared from *Chenopodium album*, spinach, beets, and mangels, and *Datura metel*. *P. betae* has been reared from the same hosts except *D. metel* (Solanaceae). This agrees with the European work in that *betae* is restricted to Chenopodiaceae, whereas *hyoscyami* is not.

More interesting, however, is the fact that all specimens of *hyoscyami* that I have seen are from the eastern half of North America whereas *betae* occurs commonly in the West, and less abundantly in the East. Specimens collected from Manitoba westwards appear to be entirely of *betae*, and one small series from Ontario and two from New York are also of *betae*. Huckett figured the ovipositor of *betae* in 1921, and the hypopygium of *betae* in 1924, when referring to *hyoscyami*. It is probable that all western and many eastern references to *P. hyoscyami* in the literature should properly be credited to *P. betae*. Whether *hyoscyami* or *betae* is the commoner species in the East can only be determined by further studies. Further studies are also needed to ascertain whether there are any significant differences in the biology of these two species on beets and spinach.

Economic Status in Canada

The miners are of considerable economic importance, particularly where spinach is grown commercially. Records received by Mr. C. G. MacNay, in charge of the Canadian Insect Pest Record, gave the following information (personal communication): They caused serious damage to spinach crops in 1956-57 in British Columbia; in 1951-52 in Manitoba; and in 1925-27, 1931, 1950, and 1956-57 in some areas of Ontario and Quebec. The damage to beets, sugar

beets, and mangels is less serious, since the foliage is not commonly used for food by humans. These plants usually recover from the first severe infestations, produce new leaves, and make up the growth lost. In only a few cases has severe stunting resulted from attacks of these flies. Serious leaf damage to these crops occurred during June in western Canada in 1941-44 and 1956-57, and in eastern Canada in 1903, 1913, 1917-18, 1924-28, 1950, and 1955.

Summary

In North America the spinach leaf miner, formerly known as *Pegomyia hyoscyami* (Panzer) represents two species, *P. hyoscyami* and *P. betae*, a species previously known only from Europe. *P. hyoscyami* is apparently strictly eastern in distribution, whereas *P. betae* is widespread, and is undoubtedly the species referred to in all reports of Western Canadian outbreaks. *P. hyoscyami* has contiguous male parafrontals, a broad vitta on the female abdomen, a short broad surstylus, and weakly sclerotized female eighth sternum, and is common on many plants of Chenopodiaceae and Solanaceae. *P. betae* has distinctly separated male parafrontals, a very weak vitta on the female abdomen, an elongate, slender surstylus, and strongly sclerotized female eight sternum, and is apparently restricted to plants of Chenopodiaceae. A history of recorded outbreaks in Canada is given, as well as a summary of published data on the life-history and host plants of the two species.

Acknowledgements

I would like to thank Mr. W. G. Matthewman, Crop Insect Section, Entomology Laboratory, Ottawa, Ontario, and Dr. R. A. Dunning, Dunholme Field Station of the Rothamsted Experimental Station, Dunholme, England, for the material and information which prompted me to undertake the study; and Dr. R. H. Foote of the United States National Museum, Washington, D.C., for the selection and loan of specimens from that institution.

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Studies of the Byron Bog in Southwestern Ontario X. Inquilines and Victims of the Pitcher-Plant, *Sarracenia purpurea* L.[1]

By W. W. JUDD[2]

In the description of the Byron Bog (Judd, 1957a) it was pointed out that the pitcher-plant, *Sarracenia purpurea* L., is to be found in the *Chamaedaphnetum calyculatae* association in the bog. The period of blooming of this plant in 1956 was from June 13 to June 22 (Judd, 1958). In that year rearings were made of larvae of the moth *Exyra rolandiana* on the flowers and leaves of the plant (Judd, 1957b). Also in 1956 a study of the inquilines and victims to be found in the leaves of the plant was undertaken, based upon a series of daily collections of insects and other arthropods from the leaves. The present paper is a report on this project.

Succession of Events in the Growth of *Sarracenia*

Observations on the pitcher-plants were begun on May 15, 1956. At that time the only plants in evidence were those that had grown in 1955, each plant consisting of a dead flower stalk standing upright in the bog and a cluster of

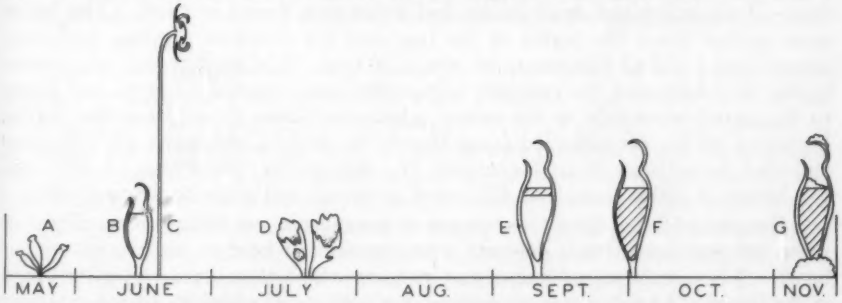

Fig. 1. Succession of events in the growth of *Sarracenia purpurea*. A, Young leaves of 1956 growing through May and June; B, First leaves of 1956 open on June 14; C, Blooming of flowers, June 13 to June 22; D, Leaves of 1955 rotted away by July 21; E, First shell ice on water in leaves of 1956 on September 10; F, First solid ice in leaves of 1956 on October 1; G, First snow on bog on November 10.

leaves encircling the base of this stalk. The leaves were still intact, having passed through the winter without collapsing, and were filled with water. During May and most of June they remained intact but after that they gradually rotted away. Typically, a leaf turned brown and withered at its tip and this withering progressed downward through the length of the leaf till eventually the leaf tissue had been reduced to gummy, black slime which fell away to the ground, releasing the water from the leaf and leaving only a short length of stalk at the base. By July 21 all leaves of 1955 had rotted away (Fig. 1, d).

The leaves of 1956 first appeared after the middle of May as short, reddish blades about one-half inch long. They continued their growth during May and June (Fig. 1, a) and the first leaves to open at their upper ends and thus give access to the chamber within did so on June 14 (Fig. 1, b). The flower bud appeared as a small red knob in the centre of the cluster of leaves. The buds enlarged and the stalks elongated rapidly so that the flowers came into

[1]Contribution from the Department of Zoology, University of Western Ontario; a project supported by funds from the government of Ontario granted through the Ontario Research Foundation.

[2]Associate Professor of Zoology; the collections were made and the data assembled while the writer held a Summer Research Associateship of the National Research Council in 1956.

bloom between June 13 and 22 (Fig. 1, c) with the maximum blooming on June 17 (Judd, 1958). The leaves enlarged to their full stature and held water throughout the season. The first shell ice occurred on the surface of the water in the leaves on September 10 (Fig. 1, e) and thereafter the water in the leaves frequently froze at the surface, particularly during the night and early morning; and on October 1 all the water was frozen solid in the leaves (Fig. 1, f). The water alternately thawed and froze till November 10 when the first snow fell on the bog (Fig. 1, g) and thereafter the water remained frozen most of the time.

During the development of the plants there were 38 days, from June 14 to July 21, in which some leaves of 1955 were intact and the leaves of 1956 were open. Thus there was a period of more than a month in which populations of inquilines could exist in the leaves of both years simultaneously and a transfer of populations from leaves of 1955 to those of 1956 could be effected. Inquilines were first found in the leaves of 1956 on June 21, one week after the opening of the first leaves on June 14.

Methods

The procedure followed in 1956 was to collect each day, from May 15 to November 15, from three to six intact leaves of *S. purpurea* and remove from them all the living and dead insects and arthropods found in them. The leaves were picked from the plants in the bog and the contents of each leaf were poured into a vial of dimensions 85 mm. x 20 mm. The corked vials were taken to the laboratory and the contents were sorted and counted. Larvae and pupae to be reared were left in the water which had been taken from the leaves. Leaves of 1955 were collected from May 15 to July 21 and leaves of 1956 were collected from June 21 to November 15. Altogether, 207 leaves of 1955 and 282 leaves of 1956, a total of 489, were collected and their contents studied.

Samples of living larvae and pupae of mosquitoes and midges were reared at room temperature in vials covered with cheesecloth held in place with rubber bands. They were reared first in the water in which they were originally found in the leaves. As this water evaporated, tap water was added to keep a sufficient volume in the vial and still leave sufficient air space above the water for the emerged adults to move about in. Larvae of sarcophagid flies were reared on loose wads of sphagnum moss taken from the bog and put in rearing vials with water. Dead insects etc. in the debris at the bottom of the chamber in each leaf were sorted out, counted and identified insofar as their state of preservation permitted. Sclerites of disintegrated insects were also kept to aid in estimating the numbers of insects which had fallen victim to the leaves.

Most of the arthropods found in the leaves were identified by the following taxonomists who, unless otherwise noted, are on the staff of the Division of Insect Identification and Parasite Introduction of the U.S. Department of Agriculture: P. H. Arnaud (*Metriocnemus*), E. W. Baker (Anoetidae), B. D. Burks (Eulophidae), N. B. Causey, Fayetteville, Arkansas (Diplopoda), E. A. Chapin (Coccinellidae), H. R. Dodge, Forest Insect Laboratory, Missoula, Montana (Sarcophagidae), C. F. W. Muesebeck (Braconidae, Ceraphronidae), W. R. Richards, Department of Agriculture, Ottawa (Cercopidae), J. G. Rozen (Helodidae), R. I. Sailer (Nabidae), M. R. Smith (Formicidae), T. J. Spilman (Cantharidae, Lycidae, Elateridae), A. Stone (Lycoriidae, Silvicolidae), F. A. Urquhart, Royal Ontario Museum, Toronto (Gryllidae), G. B. Vogt (Chrysomelidae), L. M. Walkley (Ichneumonidae), R. E. Warner (Dytiscidae, Curculionidae, Hydrophilidae), D. A. Young (Derbidae). Other insects were identified by the writer using appropriate keys, e.g., Carpenter and LaCasse (1955) for mosquitoes.

Inquilines in the Leaves of *Sarracenia*

Acarina

Anoetidae

***Histiostoma* sp.**

These mites were first noted, in leaves of 1955, on June 8 and were prevalent in leaves of 1955 thereafter. They were the first inquilines to appear in leaves of 1956, being present on June 21, one week after the leaves of 1956 first opened on June 14. They moved actively about in the water in the chambers of the leaves. A likely source of food for the mites was the mass of decaying insects in the leaves, for Baker and Wharton (1952) and Banks (1905) state that mites of the genus *Histiostoma* occur in decaying materials. Specimens have been retained in the United States National Museum.

Diptera

Tendipedidae

***Metriocnemus* sp.**

The common pitcher-plant midge of eastern North America, *Metriocnemus knabi* Coquillett, was described by Coquillett (1904) from specimens reared by Knab (1905), and its larva was described by Knab (1905) and Johannsen (1905). In determining the material from the Byron Bog, Dr. Arnaud pointed out that a revisional study of genitalia would be necessary before a positive determination would be possible.

Larvae of *Metriocnemus* were prevalent in the leaves of the plants in the Byron Bog throughout the season and were collected from 47 per cent of the leaves of 1955 and 43 per cent of the leaves of 1956 (Table I). The number of larvae per leaf ranged from one to 35 (Table I) with numbers below six occurring most commonly. They were found mainly squirming about in the mass of dead insects in the leaves but were capable also of swimming freely in the water with a wriggling motion. They were present in the leaves of 1955 as long as these leaves lasted (Fig. 2, a, b) and they turned up first in the leaves of 1956 on June 22, eight days after the first of these leaves opened on June 14. The population in the leaves built up slowly thereafter, reaching a maximum at the end of October and in November (Fig. 2, c, d). Larvae found frozen in the ice in leaves after September 10 became immediately active after the ice melted. Knab (1905) reports rearing adults from larvae which had been found frozen in leaves in the spring. No pupae were collected from the leaves.

In preparation for pupation the larvae crawled up the side of the vials above the surface of the water and each larva produced a flat patch of clear jelly adhering to the glass. This patch was about half an inch high and triangular in shape with one angle of the triangle directed upward and the base of the triangle resting on the water. The larva pupated in the jelly with its anterior end upward. When preparing to emerge the pupa wriggled upward in the jelly leaving a narrow tube one mm. wide through the jelly and then the adult emerged from the tube at the upper angle of the triangle. Knab (1905) and Usinger (1956) show the jelly mass produced by *M. knabi* as being typically elongate oval in shape. The triangular shape, described in the present study, was probably the result of the larvae having to produce the jelly masses against the smooth surface of the glass vial.

Thirty-eight midges were reared through from the larval to the adult stage in the vials (Table II), so the duration of the pupal stage was known. It ranged from one to six days with two and three days being the most frequent. Knab (1905) found that adult *M. knabi* emerged two or three days after pupation. In addition, several other adults emerged to give a total of 54 adults reared:—

TABLE I

Distribution of larvae of insects in leaves of *Sarracenia purpurea*

																													Total Larvae	Total Leaves	Larvae per Leaf	Number of Leaves Occupied	Percent of Leaves Occupied
Metriocnemus sp.:																																	
Larvae per leaf	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	30	35	40					
Leaves of 1955:																																	
Frequency	109	40	16	10	8	5	3	4	3	0	2	2	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0		207		98	47
No. of larvae	0	40	32	30	32	25	18	28	24	0	20	22	12	0	0	0	0	0	18	0	0	0	22	0	0	0	0	60	0	0	383		1.9		
Leaves of 1956:																																	
Frequency	161	42	17	12	7	12	2	2	4	3	5	0	4	0	0	1	1	0	1	0	1	0	1	0	1	0	1	2	2	0		282		121	43
No. of larvae	0	42	34	36	28	60	12	14	32	27	50	0	48	0	0	15	16	0	18	0	20	0	22	0	24	0	26	60	70	0	654		2.3		
Wyeomyia smithii:																																	
Larvae per leaf	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	30	35	40					
Leaves of 1955:																																	
Frequency	68	36	28	16	12	8	6	9	3	3	6	1	4	1	0	2	0	0	0	0	1	0	0	0	0	1	0	2	0	0		207		139	67
No. of larvae	0	36	56	48	48	40	36	63	24	27	60	11	48	13	0	30	0	0	0	0	20	0	0	0	0	25	0	60	0	0	645		3.1		
Leaves of 1956:	123	24	27	20	14	10	16	10	4	6	3	1	6	1	0	6	1	2	0	0	2	0	0	1	0	1	1	1	1	1		282		159	57
No. of larvae	0	24	54	60	56	50	96	70	32	54	30	11	72	13	0	90	16	34	0	0	40	0	0	23	0	25	26	30	35	40	981		3.5		
Sarcophagidae:																																	
Larvae per leaf	0	1	2	3																													
Leaves of 1955:																																	
Frequency	201	6	0	0																												207	
No. of larvae	0	6	0	0																											6		0.03	6	3
Leaves of 1956:																																	
Frequency	191	85	2	4																												282	
No. of Larvae	0	85	4	12																											101		0.4	91	32

19 ♂ ♂ (35%) and 35 ♀ ♀ (65%) distributed as follows – 1955 leaves: 13 ♂ ♂, 26 ♀ ♀; 1956 leaves: 6 ♂ ♂, 9 ♀ ♀. Six males and four females are deposited in the United States National Museum.

Culicidae

***Wyeomyia smithii* (Coquillett)**

This species was described by Coquillett (1901) from material bred by Smith in New Jersey. Larvae were prevalent in the leaves of the plants in the

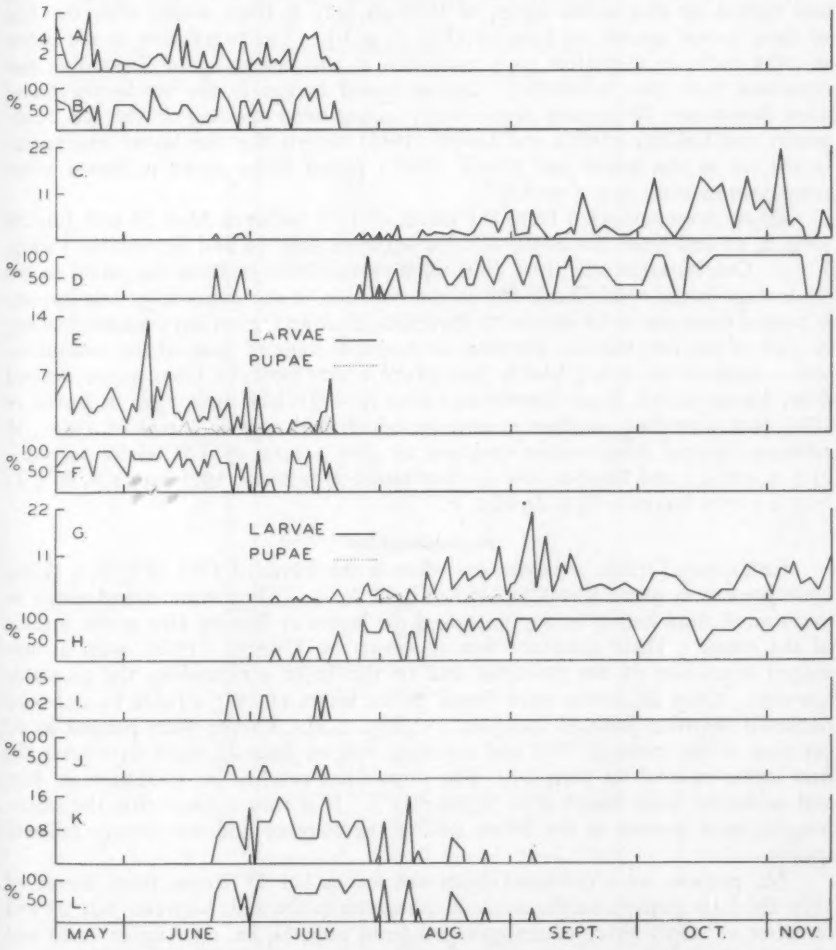

Fig. 2. A-D, *Metriocnemus* sp.: A, Number of larvae per leaf in leaves of 1955; B, Percentage of leaves of 1956 occupied by larvae; C, Number of larvae per leaf in leaves of 1956; D, Percentage of leaves of 1956 occupied by larvae. E-H, *Wyeomyia smithii*: E, Number of larvae and pupae per leaf in leaves of 1955; F, Percentage of leaves of 1955 occupied by larvae and pupae; G, Number of larvae and pupae per leaf in leaves of 1956; H, Percentage of leaves of 1956 occupied by larvae and pupae. I-L, Sarcophagidae: I, Number of larvae per leaf in leaves of 1955; J, Percentage of leaves of 1955 occupied by larvae; K, Number of larvae per leaf in leaves of 1956; L, Percentage of leaves of 1956 occupied by larvae.

Byron Bog through most of the season (Fig. 2, e, g) and were collected from 67 per cent of the leaves of 1955 and 57 per cent of the leaves of 1956 (Table I). The number of larvae per leaf ranged from one to 40 with numbers below 10 predominating. The figures of 3.1 larvae per leaf in leaves of 1955 and 3.5 larvae per leaf in leaves of 1956 (Table I) approximate the average figure of four or more per leaf given by Haufe (1952). They were found swimming actively in the water or motionless at the surface hanging head downward. They were present in the leaves of 1955 as long as these leaves lasted (Fig. 2, e, f) and turned up first in the leaves of 1956 on July 6, three weeks after the first of these leaves opened on June 14 (Fig. 2, g, h). The population in the leaves of 1956 built up thereafter to a maximum at the beginning of September and remained high into November. Larvae found frozen in the ice in the leaves after September 10 became immediately active after melting of the ice. Carpenter and LaCasse (1955) and Lloyd (1942) record that the larvae overwinter in the ice in the leaves and Haufe (1952) found them active in leaves when temperatures were near freezing.

Pupae were collected from the leaves of 1955 between May 18 and July 19 (Fig. 2, e) and from the leaves of 1956 between July 26 and September 1 (Fig. 2, g). One hundred and forty-four were reared through from the larval to the adult stage in the vials (Table II), so the duration of the pupal stage was known. It ranged from one to 18 days with durations of six and seven days predominating. In view of the fact that the duration of the pupal stage of most of the mosquitoes was a week or less it is probable that adults which emerged from pupae derived from larvae which overwintered in leaves of 1955 laid their eggs in leaves of 1955, thus providing another generation which laid eggs in leaves of 1956. In addition, several other adults emerged to give a total of 179 adults reared:– 73 ♂ ♂ (41%) and 106 ♀ ♀ (59%) distributed as follows: 1955 leaves – 41 ♂ ♂, 74 ♀ ♀; 1956 leaves – 32 ♂ ♂, 32 ♀ ♀.

Sarcophagidae

Sarcophagid larvae were not prevalent in the leaves of 1955 (Fig. 2, i, j) but were present in many leaves of 1956 (Fig. 2, k, l). They were found either in the mass of dead insects in the bottom of the leaves or floating free at the surface of the water. Their structure was as shown by Usinger (1956) with a cup-shaped expansion of the posterior end of the body surrounding the posterior spiracles. Only six larvae were found in the leaves of 1955 (Table I) and they occurred between June 25 and July 18 (Fig. 2, i). Larvae were present in 32 per cent of the leaves of 1956 and appeared first on June 22, eight days after the first leaves opened on June 14. The population reached its maximum in July and no larvae were found after September 5. It is thus evident that the sarcophagids were present in the leaves during the summer and not during fall and spring.

No puparia were collected from the leaves but 15 larvae from leaves of 1956 did form puparia on the wads of sphagnum in the vials between July 23 and October 4. Only three adults emerged from puparia, i.e. on August 7, 14 and 15, after being in the pupal stage for 14 or 15 days (Table II). They were *Fletcherimyia fletcheri* (Ald.), one of six species which Aldrich (1916) records as being reared from *Sarracenia*.

Victims in the Leaves of *Sarracenia*

In most of the leaves collected there was a mass of dead organisms in the bottom of each leaf and, in some cases, live non-inquiline insects still struggling in the water. These were counted and identified. The mass of material, parti-

TABLE II

Duration of pupal stage of insects from leaves of *Sarracenia purpurea*

Number of Days	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total pupae reared to adult
Metriocnemus sp.:																			
Leaves of 1955	5	10	9	2	0	1													27
Frequency Leaves of 1956	2	5	3	0	0	1													11
Both years	7	15	12	2	0	2													38
Wyeomyia smithii:																			
Leaves of 1955	3	1	5	9	11	21	28	4	2	4	2	3	0	1	0	0	0	4	98
Frequency Leaves of 1956	2	3	2	8	8	15	4	1	1	1	0	1	0	0	0	0	0	0	46
Both years	5	4	7	17	19	36	32	5	3	5	2	4	0	1	0	0	0	4	144
Sarcophagidae:																			
Frequency Leaves of 1956														1	2				3

cularly in the leaves of 1955, also included dissociated sclerites of insects and other arthropods such as heads, thoracic skeletons, abdominal segments, wings and legs. These were sorted out and identified as far as possible. The numbers of the several organisms, including the minimum number of individual organisms which could be deduced as having been present from examination of remains such as sclerites, wings, segments, etc., are shown in Table III.

Almost half the organisms in the leaves were large calyptrate flies, followed in relative abundance by ants (Formicidae), lady-beetles (Coccinellidae), other flies, blow flies (Calliphoridae – many flies of this family are probably also included among the calyptrate flies) and other beetles. The other organisms represented were present in lesser numbers. Wray and Brimley (1943) studied the victims of *Sarracenia flava* in North Carolina and found large numbers of ants, lady-beetles and calliphorid flies as well as lesser numbers representing other orders and families and they concluded that calliphorid flies are evidently attracted to the leaves by the odour of decaying insects.

The masses of dead organisms in the leaves of 1955 gave no indication of the succession in which the insects entered the leaves through the season. Victims of the leaves of 1956 were first found on June 22, eight days after the first leaves opened on June 14. They were two small, green midges and a click beetle, the latter still alive when found. The following list shows the succession in which the various organisms first appeared in the leaves of 1956 (genera denoted by an asterisk (*) were represented in the collections made by Wray and Brimley (1943) in North Carolina):

June 22–Adult midges (Diptera: Tendipedidae)
–*Ampedus* sp. (Coleoptera: Elateridae)
June 23–*Cremastus* sp. (Hymenoptera: Ichneumonidae)
June 26–Calyptrate flies
June 27–Ants (Hymenoptera: Formicidae)
June 28–*Myrmica lobicornis fracticornis* Emery (Hymenoptera: Formicidae)
June 29–Mosquito (Diptera: Culicidae)
–Small beetle (Coleoptera)
June 30–*Gymnaetron antirrhini* Payk. (Coleoptera: Curculionidae)
July 3–*Cyphon* sp. (Coleoptera: Helodidae)
July 4–Moths (Lepidoptera: Tortricidae)
July 6–*Adopoea lineola* Ochs. (Lepidoptera: Hesperiidae)
July 13–*Apanteles ensiger* Say (Hymenoptera: Braconidae)
–*Chrysocharis* sp. (Hymenoptera: Eulophidae)
July 14–Plant bug (Heteroptera: Miridae)
July 16–"Woolly bear" caterpillar (Lepidoptera: Arctiidae)
July 21–Bug (Heteroptera: Nabidae)
–Lady-beetle (Coleoptera: Coccinellidae)
July 25–*Silvicola marginata* (Say) (Diptera: Silvicolidae)
–*Cantharis** sp. (Coleoptera: Cantharidae)
July 26–*Philaenus leucophthalmus* (var.) (Homoptera: Cercopidae)
July 27–Horse fly (Diptera: Tabanidae)
July 31–Bark louse (Corrodentia)
Aug. 9–Plant louse (Homoptera: Aphidae)
–*Pollenia rudis* (Fabr.) (Diptera: Calliphoridae)
Aug. 14–*Clastoptera saint-cyri** (var.) (Homoptera: Cercopidae)
–*Galerucella* (*vaccinii* Fall?)* (Coleoptera: Chrysomelidae)
Aug. 16–*Graphops.* sp. (Coleoptera: Chrysomelidae)

TABLE III
Number of victims in leaves of *Sarracenia purpurea*

		Leaves of 1955	Leaves of 1956	Total
Diplopoda		0	3	3
Araneida		18	6	24
Collembola		1	0	1
Corrodentia		1	1	2
Coleoptera:	Carabidae	1	3	4
	Dytiscidae	1	0	1
	Staphylinidae	0	1	1
	Hydrophilidae	0	1	1
	Helodidae	2	3	5
	Lycidae	0	1	1
	Cantharidae	1	1	2
	Elateridae	4	1	5
	Coccinellidae	22	52	74
	Chrysomelidae	3	3	6
	Curculionidae	5	2	7
	Other beetles	32	15	47
	Beetle larvae	1	0	1
Orthoptera:	Gryllidae	17	9	26
	Tettigoniidae	0	1	1
Lepidoptera:	Hesperiidae	0	1	1
	Phalaenidae	0	4	4
	Tortricidae	1	6	7
	Other moths	1	4	5
	Arctiidae — larva	0	1	1
	Geometridae — larva	1	0	1
Heteroptera:	Piesmidae	1	0	1
	Miridae	1	1	2
	Nabidae	0	6	6
Heteroptera:	Pentatomidae	0	1	1
	Other bugs	4	1	5
Homoptera:	Cercopidae	1	8	9
	Derbidae	1	0	1
	Cicadellidae	0	4	4
	Aphidae	0	2	2
	Other hoppers	20	4	24
Neuroptera:	Chrysopidae	1	0	1
Diptera:	Culicidae	4	6	10
	Tendipedidae	1	9	10
	Lycoriidae	1	0	1
	Sylvicolidae	0	5	5
	Tabanidae	2	3	5
	Syrphidae	2	1	3
	Sarcophagidae	3	0	3
	Anthomyiidae	9	0	9
	Calliphoridae	0	57	57
	Calyptrate flies	118	389	507
	Other flies	16	64	80
Hymenoptera:	Braconidae	0	1	1
	Ichneumonidae	0	1	1
	Eulophidae	0	1	1
	Ceraphronidae	1	0	1
	Vespidae	1	1	2
	Apidae	0	1	1
	Formicidae	31	66	97
	Other wasps	6	8	14
TOTAL		336	759	1,095

Aug. 17–*Plateros** sp. (Coleoptera: Lycidae)
Aug. 21–Nymph of stink bug (Heteroptera: Pentatomidae)
Aug. 22–*Labidomera clivicollis* Kirby (Coleoptera: Chrysomelidae)
Aug. 25–*Polyzonium bivirgatum* Wood (Diplopoda: Polyzoniidae)
Aug. 30–*Nemobius fasciatus* Scudd.* (Orthoptera: Gryllidae)
Aug. 31–Moth (Lepidoptera: Phalaenidae)
Sept. 1–Leaf hopper (Homoptera: Cicadellidae)
Sept. 5–*Casnonia pennsylvanica* L. (Coleoptera: Carabidae)
Sept. 15–Spider (Araneida)
Sept. 22–Hover fly (Diptera: Syrphidae)
Oct. 4–Rove beetle (Coleoptera: Staphylinidae)
–Grasshopper (Orthoptera: Tettigoniidae)
Oct. 6–*Nabus ferus* (L.)* (Heteroptera: Nabidae)
Oct. 23–Water scavenger beetle (Coleoptera: Hydrophilidae)
Nov. 5–Wasp (Hymenoptera: Vespidae)

In addition to the organisms mentioned in the foregoing list the following identified insects were found in the leaves of 1955:

Coleoptera: Elateridae–*Aeolus m. mellilus* (Say)
Coccinellidae–*Coccinella trifasciata* L.
Curculionidae–*Endalus* sp.
Homoptera: Derbidae–*Cedusa* sp.
Diptera: Culicidae–*Chaoborus flavicans* (Meigen)
Lycoriidae–*Bradysia* sp.
Hymenoptera: Ceraphronidae–*Megaspilus fuscipennis* Ashm.
Formicidae–*Camponotus noveboracensis* Fitch*
–*Myrmica emeryana* Forel
–*Myrmica* sp.
–*Tapinoma sessile* (Say)

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Flight Responses to Various Sounds by Adult Males of *Aedes aegypti* (L.) (Diptera: Culicidae)[1]

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Many authors observed that mosquitoes respond to a large variety of artificial sounds (for references see Roth, 1948). Efforts to attract males of *Aedes aegypti* (L.) by play-back recordings of the flight sound of the female have met with moderate success (Kahn *et al.*, 1945; Offenhauser and Kahn, 1949; Kahn and Offenhauser, 1949). Roth (1948) demonstrated that males of *A. aegypti* approached the sounds of tuning forks and sine sounds from a speaker. He also determined the upper and lower limits of frequencies that stimulated males, but in these experiments he did not use attraction to the source of the sound as the criterion of response, but the "seizing and clasping" reaction. He exposed the male mosquitoes in cages, three inches by three inches by one inch, placed against a box that housed a loud speaker. Under these conditions the mosquitoes had little opportunity to fly to orient themselves toward the sound source. Moreover the sound used was of such intensity (108 db at 2½ inches) that the whole cage vibrated, so that at least part of the response was undoubtedly caused by vibration of the substratum on which the mosquitoes rested. Sounds of such intensity do not normally occur in the natural environment of the mosquito. Moreover, the "seizing and clasping" response does not occur until the male approaches the female in response to sound or other stimulus. If the place of sound in the attraction of the males is to be studied, the primary response, that of approach, should be the criterion and the amount of sound used should bear a reasonable relation to that occurring in nature.

Kahn *et al.* (1945) stated that the sounds produced by mosquitoes are of three kinds: the noises made by the wings when they are in flight; the beating of the wings while at rest; and the rubbing of the tarsi against the wings. They also referred to "certain bird-like sounds the origin of which was not determined." The last were not noted by other workers or in the present study; they may have been produced in the apparatus because of the high amplification used. A sound is produced by any movement of an insect on the substratum or when one part of the body is rubbed against another, but it is doubtful if it has biological significance unless it occurs regularly or is connected with some pattern of behaviour. The behaviour of the males in the presence of the flight sound of the female leaves little doubt of its significance. The question arises as to whether it is specific, especially as *A. aegypti* and other species respond to a variety of other sounds. Tishner (1953) stated in effect that for *Anopheles subpictus* Grassi the flight sound of the female was not only significant to the male but was specific. He (p. 339, translated) generalized in the following statement: "Nature pays strict attention to the separation of species. As the flight sound pitch, according to the observations of Soltavatta (1947), is practically the same for all species of mosquitoes — other differentiating characteristics must exist for the flight sound of the individual species". In a later paper (Tischner, 1955), however, he illustrates two examples of attraction of mosquitoes to sounds other than the flight sound of the same species. As mosquitoes do respond to sounds other than the "calling" of the opposite sex of the same species there are two possible explanations: the other sounds that are at-

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tractive contain components sufficiently similar to the natural sounds to cause a response or all sounds to which they respond contain a single or a very few attractive elements. The diversity of evidence presented and of the opinions expressed by previous workers appeared to warrant a further examination of this and other aspects of the subject.

Materials and Methods

A. aegypti was reared in the laboratory by methods conventional for this species (Trembley, 1935). Males were separated from the females in the pupal stage and allowed to emerge in a cage. The frame of this cage and of all others used in the tests was of wood, with the inside dimensions of 10¾ x 11 x 16½ inches high. Three sides and the top were of plastic screen; the bottom was of Masonite (International Fibre Board and Plywood Sales, Ltd., Gatineau, Que., Canada) and the front of $\frac{1}{16}$-inch clear plastic with a 1⅞-inch hole in the centre, normally closed by a cork. The adults that emerged on the second day after pupation were used in the experiments so that the mosquitoes were up to 24 hours old at the beginning of a series of tests. For the tests, 60 mosquitoes were placed in each of the required number of cages. After each day's tests, the mosquitoes were returned to the stock cages and reapportioned to cages for the next day's tests. Mortality during the tests was compensated for by starting with a stock approximately double that required for a complete series of tests. The test cages were kept in a soundproof room except when the mosquitoes were being subjected to a signal. This room was lighted by a single 15-watt lamp and the temperature was kept at 75°F. The cages were covered with wet cloths between tests.

Fig. 1 indicates the arrangement of the apparatus used in the tests. The mosquitoes were exposed by placing the test cage (A), with the cork removed, against the wooden ring (C), behind which was the driver-type loud speaker (B). Any mosquitoes approaching the source of the sound were sucked into the counting tube (D). A relief valve and a manometer (not shown) were incorporated into the vacuum line to reduce variations in the suction. After exposure of mosquitoes to a signal, the counting tube was removed and the mosquitoes in it counted and returned to the test cage by blowing. Each signal was sounded for five seconds, preliminary experiments having shown this time to be most effective for practical purposes. As fewer mosquitoes were trapped as light intensity was increased, a constant intensity of 6.5 candles per square foot was maintained on the top of the cage. This amount of light did not interfere with the response of the mosquitoes and was adequate for working. The temperature of the laboratory was maintained at between 75 and 80°F. and the relative humidity, supplied by a vaporizer-type humidifier, at from 64 to 80 per cent. In each series of tests the number of cages used was equal to the number of different sounds being tested. For example, where eight frequencies were being tested the first of the eight cages was exposed at the lowest frequency, then cage No. 2 at the next higher frequency and so on to the end of the series. After a 10-minute rest, the next series was commenced by testing cage No. 1 at the frequency previously used for cage No. 2. This procedure was continued until each cage had been tested at each frequency. Thus each signal was first tested on a "fresh" cage, then on a cage that had been subjected to a signal once previously, and so on. As the experiments were designed to assess the response of mosquitoes in flight, the sides and top of the cages were brushed to ensure flight immediately before a signal was commenced.

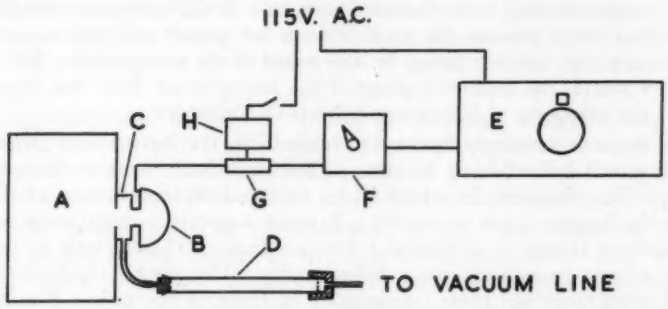

Fig. 1. Block diagram of the arrangement of the apparatus used while testing the response of the males of *Aedes aegypti* (L.) to sounds of various frequencies and intensities. A, test cage; B, driver-type loud speaker (Atlas Sound Corp., 1443 39th St., Brooklyn 18, N.Y., Model PD5VH, response 80-9000 c/s); C, wooden ring; D, counting tube, clear plastic, 1 5/16 by 15 inches; E, sine-wave generator (Measurement Engineering Ltd., Arnprior, Ont., Model AG-2); F, calibrated volume control; G, relay; H, automatic timer (Industrial Timer Corp., 1407 McCarter Highway, Newark 4, N.J., Type P49).

An intensity of 75 db at one inch from the loud speaker, demonstrated as optimum in preliminary experiments, was maintained in all frequency tests and in all experiments where intensity was not being investigated, unless otherwise stated. All sound level measurements were made with a sensitive meter [a] and calibration was done with the loud speaker in an insulated box in the soundproof room (approximately 60 db down at 500 c/s).

A comparison of the response to sound by resting and flying males of *A. aegypti* was made by placing cages with a single male in the testing position. When the male came to rest a five-second exposure to a sine sound of 500 c/s at 85 db was made. If the mosquito took to flight it was considered to have responded. Then the mosquito was caused to fly and the same sound presented. If the mosquito was caught in the trapping device the response was considered positive.

The frequency of the fundamental tone of the flight sound of females was determined by aural comparison. Single females were induced to fly in cages containing a microphone, and the sound was fed through an amplifier to an earphone. Another earphone was attached to a variable signal generator and the tones were matched. Roth (1948) pointed out the difficulties of determining frequency by aural comparison, but indicated that octave errors were most common. In the present work enough sounds were recorded and analysed to eliminate this type of error; when the range is determined, aural comparison can be made with a considerable degree of accuracy.

The intensity experiments were conducted at a frequency of 500 c/s. The intervals of 17 db in the sound levels used represent a power factor of 50. To determine the loudness of the sound of a single mosquito in flight, tethered females were placed half an inch from the microphone of the sound-level meter in the insulated box in the soundproof room. In the box was placed a small speaker attached to an audio signal generator controlled from the outside, as to volume and frequency. This provided a standard background of the approximate frequency of the flight sound of the mosquito. By trial and

[a]Type 410 - C, Hermon Hosmer Scott, Inc., 385 Putnam Ave., Cambridge 39, Mass., U.S.A. Sound Level Range: 34 to 140 db above the standard ASA reference level of 0.0002 dynes per square centimeter r.m.s.

error, a volume setting was obtained such that if the mosquito and the background were both present the total volume of sound was twice that of the background alone, or three db up. As the sound of the mosquito was half the total amount of sound, the decibel reading of the background alone was equal to the sound of the mosquito at half an inch from the microphone.

The distance a male mosquito was "called" by the flight sound of the female was determined by tethering females in a room where there were many males in flight. The distances at which males changed their direction of flight and came to the females were estimated. A more accurate measurement was made by tethering a female at a measured distance from a 1¾-inch hole in the plastic front of a cage containing many flying males. The plastic blocked the sound from all mosquitoes but those immediately in front of the hole. The maximum distance from the hole that males were attracted to the female was, therefore, taken as the outer limit of response.

To determine what proportion of mosquitoes were unresponsive, five cages, each with 60 mosquitoes, were tested daily for 10 days at all the frequencies previously tested, commencing at a different frequency each day. Ten-minute intervals were allowed between successive tests of the same cage. The mosquitoes caught were placed in a separate cage so that finally only unresponsive mosquitoes remained in the test cages. Two replicates were tested.

The importance of the fundamental of the female flight sound was tested in three phases. First, a tape recording [4] of the flight sound of a single female was tested both in its natural form and with the fundamental of 426 c/s removed by means of a variable band-pass filter [5]. Second, separate tape recordings were made of a male and female in flight and then both were re-recorded in such a manner that the frequencies of the fundamentals were adjusted to 500 c/s (this was achieved by making the re-recording on a tape recorder for which capstans were machined to the requisite diameter). Third, a tape recording of a sine wave at a frequency of 500 c/s plus the harmonics and subharmonics of 3000, 2000, 1000, 250, and 125 c/s were tested against a similar recording from which the fundamental (500 c/s) had been omitted. In all three phases the total sound played back was 75 db, measured as described previously.

A preliminary experiment showed that the recorded sound of a motor-driven grinder which did not elicit an approach reaction in males when presented at 75 db did not prevent a normal response to a sine sound of 500 c/s presented at the same time. To test the effects of various intensities of "background" noise, an artificial noise was built up on tape by overprinting sine waves of 100, 156, and 282 c/s and square waves of 933, 1840, and 4130 c/s. Square waves were used at the upper frequencies because they contain an infinite number of harmonics, and sine waves at the lower frequencies, as some of the harmonic components of square waves at these frequencies would certainly be in the attractive region. All the frequencies were recorded at the same intensity and the composite noise was then reproduced at increasing intensities simultaneously with a sine wave of 500 c/s at 75 db. The sine wave of 500 c/s was reproduced alone as a control. The 10-decibel steps in the intensity levels of the background noise equal a power factor of 10.

(4)Recordings of mosquito sounds were made in the soundproof room with an Ampex tape recorder (Ampex Corporation, 934 Charter Street. Redwood City, California), the tape speed being altered to 15 inches per second, giving a response of 19,000 c/s. The microphone used was an Altec 633A (Altec Lansing Corp. 9356 Santa Monica Blvd., Beverley Hills, Calif.). Re-recordings to adjusted frequencies were made with a Magnemite 610 tape recorder (Amplifier Corporation of America, 398 Broadway, New York, N.Y.).

(5)Krohn-Hite, Model 310-AB; Krohn-Hite Instrument Company, Cambridge 39, Mass.

To determine the attraction of combinations of sounds, each of which was attractive by itself, recordings of female flight sounds were made at 455, 500, and 575 c/s. Overprints of all three and of two of them (455 and 500 c/s) were tested.

To determine the effects of various intensities of attractive sounds, two sine sounds, each attractive alone, were presented together at equal intensity and then with one of them reduced in steps of five decibels from 75 db to 55 db. The two sounds 500 and 551 c/s were tested separately as checks.

To test the specificity of the attraction of the flight sound on the male, the flight sounds of the females of five species of mosquitoes were made and then re-recorded so that the frequency of the fundamental was the same for all. These were tested with males of *A. aegypti.*

All experiments with recorded sounds were conducted in the same manner as those with sine sounds, the tape recorder play-back being through the speaker (B). The period of five seconds used for all tests was measured by the automatic timer for sounds from the generator and by using a measured length of tape for the recorded sounds.

Results and Discussion

The adequacy of the sampling method was demonstrated by the fact that as many as 80 per cent of the mosquitoes in a cage were caught when an attractive sound was presented for five seconds, whereas less than one per cent of the mosquitoes were caught in repeated five-second tests with the vacuum on but with no sound. The numbers of mosquitoes caught by vacuum alone was so small that no account was taken of them in assessing the data. The sampling method used was objective, as mosquitoes were caught or not caught and no judgement had to be applied in deciding whether a mosquito had responded. It is felt that in this respect the method is superior to Roth's (1948), where a decision had to be made on each response.

Table I shows that males of *A. aegypti* are attracted to sine sounds of from 300 to 800 c/s and that the maximum response is at 400 to 600 c/s. The data also show that response increases with age up to four or five days. All mosquitoes were exposed to all frequencies, whereas in Roth's work (1948, Tables IV and V, pp. 332 and 333) the mosquitoes were exposed to a series of decreasing or of increasing frequencies and each mosquito that responded was removed and was exposed to no other frequency to which it might have responded. In his tests with descending frequencies, practically all the responding mosquitoes responded to sounds above 525 c/s and with ascending frequencies practically all responded to those below 525 c/s, to which there are very high responses. Thus Roth's data, while indicating the upper and lower limits of response, do not indicate the most favourable frequencies or the percentages of mosquitoes that respond to the various frequencies.

In some preliminary experiments, sounds of 100 and 150 c/s attracted appreciable numbers of mosquitoes, but few were attracted at 200 and 250 c/s. The sounds at these frequencies were picked up by a microphone, amplified, and fed into an oscilloscope through a band-pass filter. Those at 100 and 150 c/s were found to contain weak sounds between 400 and 500 c/s. These undoubtedly were responsible for the response observed, for when a speaker that produced pure sine sounds was substituted no mosquitoes were trapped at 100 and 150 c/s and testing below 300 c/s was discontinued. Roth (1940) reported a considerable response below 300 c/s and some as low as 75 c/s. The differ-

TABLE I

Percentages of adult males of *A. aegypti* of various ages that were trapped on approaching the source of sine sounds of various frequencies at 75 db measured at one inch from the source

Cycles per second	Age in days									
	1	2	3	4	5	6	7	8	9	10
300	7.0*	6.3	3.2	4.6	2.6	3.7	2.5	3.0	2.4	3.4
350	16.8*	36.9	30.0	34.0	30.6	25.4	23.6	23.6	23.0	13.0
400	6.7	39.7	35.5	46.5	43.8	37.2	35.7	27.2	30.6	23.1
450	3.0	35.9	43.4	44.1	38.1	35.0	36.9	33.1	33.8	25.0
500	1.5	26.1	46.2	54.3	50.4	42.6	42.7	36.8	41.1	36.2
550	.9	13.2	37.0	43.0	56.8	44.0	42.0	42.6	45.7	37.9
600	1.5	29.0	27.6	45.5	50.4	36.2	47.0	42.5	43.0	30.8
650	.4	.8	8.4	20.6	21.5	15.8	18.2	18.6	22.1	16.1
700	0	.2	2.9	9.6	13.0	9.4	9.2	6.1	10.4	5.2
750	.4	0	.9	3.5	3.3	4.6	3.2	3.6	4.7	3.5
800	.4	0	.4	1.0	1.9	1.4	.6	.8	2.4	.3

*Solid underline, highest percentage for the frequency; broken underline, highest percentage for the age.

ence in Roth's results may have been caused by the different type of response observed or by undetected frequencies emitted by the speaker used.

Where males of *A. aegypti* were tested individually at rest and in flight with a sine sound of 500 c/s at 85 db, of 50 specimens 14 failed to respond under either condition. Two took to flight during the five-second sound period but 36 in flight approached the sound and were trapped. At the intensity of sound used in this test no seizing and clasping response was noted in resting mosquitoes but this was produced at will by increasing the volume to over 100 db, an amount similar to that used by Roth (1948) when he observed the same type of response.

The lowest frequency of the free-flight sound of the female was 449 c/s, the highest 603, and the average 493 for 15 three-to-four-day-old females tested. Goeldi (1905), using tuning forks and a zither for comparison, found the average frequency to be 480 c/s. Offenhauser and Kahn (1949) made a sound spectrogram of a female of *A. aegypti* (page 262, Fig. 5) with a fundamental of 750 c/s, which is much higher than any encountered in the present study. The average frequency found is within the range of artificial sounds that are most attractive to males, especially young males.

Table II shows that a sine sound of 500 c/s at 68-85 db is more attractive than when the intensity is higher or lower. The lowest intensity, 34 db (see note to Table II), was audible to the authors under "quiet" conditions at a distance of one inch. At intensities above 85 db, many mosquitoes were observed to approach the source of sound, but to hover at some distance from it.

A single female mosquito, under the conditions described, produced a sound intensity of 41 db at half an inch from the meter microphone. Flying

TABLE II

Percentages of adult males of *A. aegypti* of various ages that were trapped on approaching the source of a sine sound of various intensities at 500 cycles per second

Decibels at one inch	Age in days										
	1	2	3	4	5	6	7	8	9	10	Average
34*	1.1	3.3	1.2	2.7	.5	.6	2.6	2.8	.6	1.7	1.7
51	1.4	13.7	34.0	33.0	26.5	23.3	23.2	22.3	28.7	27.6	23.4
68	3.3	32.0	41.0	40.5	46.4	33.1	36.0	39.0	40.0	37.2	34.8
85	11.7†	30.3	40.3	38.9	39.1	37.1	30.8	31.3	35.5	32.2	32.7
102	10.6	21.6	14.2	19.6	20.3	18.3	14.6	16.3	19.5	14.1	17.2
119	6.9	7.7	5.6	4.4	4.9	7.3	4.6	4.7	5.9	6.7	5.9

*Note — This intensity was not an accurate measurement but was the lowest reading on the sound level meter; the sound did not produce a reading under "quiet" conditions and was estimated to be below 30 db.

†Broken underline, highest percentage for the age.

males were observed to dart toward tethered females from distances not exceeding 10 inches and, in the more accurate tests before an opening in the plastic front of a cage, from six inches. A sound of 41 db measured at half an inch from the source has an intensity of approximately 20 db at six inches. If the measurements were correct, a male of *A. aegypti* can, therefore, respond to a sound of approximately 20 db.

A small proportion (about four to seven per cent) of mosquitoes more than two days old were unresponsive. The proportion was higher in two-day-old mosquitoes, and considerably higher (27 per cent) in the one-day-old group. In spite of the precautions taken to ensure that all mosquitoes were in flight, some undoubtedly were at rest during the tests. Moreover, the test period, five seconds, undoubtedly expired before all the potentially responsive insects reached the catching device.

Early in the study it was noted that large speakers, i.e., those about 10 inches in diameter, would, with the proper intensity and frequency, attract male mosquitoes, but that the insects lost their sense of direction when they came close to the speaker, and flew about in front of it; where the source of the sound was small or of the driver type with a small opening they flew directly toward it.

Offenhauser and Kahn (1949) used a sound level in their trapping experiments "of the same general order of a fairly loud home phonograph." This is an indefinite statement and subject to a wide variety of interpretation. It would, however, be at least in the range of 95-100 db at one foot, a much louder sound than the present work shows to be effective in obtaining a close approach. The numbers of mosquitoes trapped by Offenhauser and Kahn were small, if, as is likely, large numbers were present. The present work shows that sounds loud enough to "call" *A. aegypti* males from a considerable distance prevent their close approach to the source of the sound. This may rule out the effective use of sound as an attractant to traps. However, a bimodal or trimodal sound might be used. Such a system would emit a strong sound for a few seconds, then a weaker sound, and finally a sound of an intensity that would favour close approach to the trapping device.

TABLE III

Percentages of males of *A. aegypti*, aged four to six days, trapped on approaching sources of various sounds involving manipulation of the fundamental; 60 per sample

	No. of samples	Percentage trapped
Female flight sound of 426 c/s		
natural	21	20.1
with fundamental removed	21	0.9
Male and female flight sounds adjusted to 500 c/s		
female	21	26.7
male	21	29.2
Recording of 125, 250, 1,000, 2,000, and 3,000 c/s*		
without 500 c/s	4	0.7
with 500 c/s	4	21.2

*Subharmonics and harmonics of 500 c/s.

Table III shows that the flight sound of the female without the fundamental did not attract the males, that the flight sound of the male was equally as attractive as that of the female when brought to the same fundamental frequency and that subharmonics and harmonics of a favourable sound alone had no effect, whereas when the fundamental was added normal response occurred. The increased attractiveness when the flight sound of the female was changed from 426 c/s to 500 c/s was expected as 500 c/s produced consistently greater response than 500 or 450 c/s in males four days or more old.

The components of the female flight sound, other than the fundamental, are undoubtedly produced as side effects of the wing motion by such factors as vibration of the surfaces, edges, and tips of the wings and they are thus harmonics of the fundamental. If they had significance in the attraction of the male, response should be greater to the complete sound than to the fundamental alone, and it would be expected that the other components alone would have some effect. The data show that only the fundamental is effective.

Table IV shows that mosquitoes can recognize and locate an attractive

TABLE IV

Percentages of males of *A. aegypti*, aged four to six days, trapped on approach to a sine sound of 500 c/s at 75 db with additions of noise at various intensities; 60 per sample; 18 samples per variant

	Percentage trapped
500 c/s (sine-wave) at 75 db	
without additions	38.8
with noise at 75 db added	41.8
with noise at 85 db added	33.0
with noise at 95 db added	8.1
with noise at 105 db added	1.1
*artificial noise at 75 db	0.8

*The following sounds were overprinted at the same V.U.: sine sounds 100 c/s, 156 c/s 282 c/s; square wave sounds 733 c/s, 1,840 c/s, 4,130 c/s.

TABLE V

Percentages of adult males of *A. aegypti*, four to six days old, that were trapped on approach to the flight sounds of females at different frequencies and to combinations of these; 60 per sample; 15 samples for each variant

	Percentage trapped
Female flight sound 455 c/s	15.99
Female flight sound 500 c/s	17.44
Female flight sound 571 c/s	27.11
Overprint of flight sounds 455, 500, 571 c/s	1.33
Overprint of flight sounds 455, 500 c/s	2.44

sound in the presence of considerable background noise, but that this ability breaks down if the background is loud enough. It can be concluded that background noises in nature, unless of exceptionally high intensity, interfere little with the ability of the male to "hear" the female.

Table V shows that two or more sounds that are attractive alone are not attractive when presented together at the same intensity. This explains what was observed in the laboratory: that a cage of flying females, the sound of which could be heard at a distance of 10 feet, failed to attract males loose in the room. At the same time, a single flying female or a tethered female attracted nearby males. A recording of the sound of a cage of flying females played back through the test apparatus also failed to elicit response. In this case, the sound was emitted from a point source, eliminating any possible effects caused by lack of localization of the sound. It can be concluded, therefore, that the effect of sound in bringing the sexes together is effective only in relative isolation. It was not determined why males of *A. aegypti* cannot respond where two or more favourable sounds are present at the same intensity. It appears, however, that, though capable of response over a considerable range of frequencies, the sound receptors cannot resonate to more than one frequency at the same time.

TABLE VI

Percentages of adult males of *A. aegypti*, four to six days old, that were trapped on approach to the source of two sine sounds at equal and unequal intensities; 60 per sample; 21 samples for each variant

	Percentage trapped
551 c/s, 75 db (check)	41.03
551 c/s, 75 db, 500 c/s 75 db	1.82
551 c/s 70 db, 500 c/s 75 db	10.71
551 c/s 65 db, 500 c/s 75 db	22.54
551 c/s 60 db, 500 c/s 75 db	29.68
551 c/s 55 db, 500 c/s 75 db	31.43
500 c/s, 75 db (check)	34.44

The data in Table VI show that, where there was a difference in the intensity of two favourable sounds, the males of *A. aegypti* responded to one of them, presumably to that of the greater intensity. As the intensity of one sound was diminished, the response increased until, where the disparity in intensity was 20 db, response was not significantly different from where only one sound was presented. The difference in response between the two checks is explained by the fact that, at the age at which these mosquitoes were tested, they are more responsive to the higher frequency. As the sounds produced by flying females of *A. aegypti* do not vary much in intensity, it follows that distance is the factor that determines which of two females will induce a male to approach.

When the flight sounds of the females of five species of mosquitoes (four of *Aedes*, one of *Culex*) were brought to approximately the same frequency as that for *A. aegypti*, and tests applied in the usual manner, the following percentages responded in the five-second test period: 37, 40, 28, 31, 33. The check, *A. aegypti*, attracted 29 per cent. This is contradictory to the statement of Tischner (1953), referred to earlier, and shows conclusively that frequency is the only significant part of the flight sound. Visual and aural demonstration of this was noted on several occasions in the laboratory during the recording of the flight sounds of different species of *Aedes* and *Culex*. Free males of *A. aegypti* came to females of other species as readily as to those of *A. aegypti*.

Offenhauser *et al.* (1948) stated that all mosquito sounds are warble-modulated. This is undoubtedly so to the human ear, but it is extremely difficult to prove or disprove. All recordings, whether of the sounds of free-flying or tethered insects, are modulated to some extent by the rapid changes in position of the insect in relation to the microphone. Because the males respond equally well to artificial sounds as to natural sounds, the effects of modulation are best studied with artificial sounds that can be modulated at will as to frequency or intensity. It was found that modulating the sound, in either frequency or intensity, at a rate of five modulations or less per second had no appreciable effect on increasing or decreasing the response to a favourable sound, but that higher modulation rates (of 10 to 25 times per second) reduced the response.

Summary

Males of *Aedes aegypti* in flight were trapped on approaching the source of sine sounds of 300 to 800 c/s, the largest percentages, 54 to 57, being trapped at 500-550 c/s. The frequency at which the greatest number were trapped increased slightly with age up to four or five days. At 500 c/s the males were attracted to intensities of 34 to 119 db, up to 46 per cent being trapped at 68 db and up to 37 at 85 db. Sounds originating from a point were more effective in producing a close approach than those from diffuse sources. The female in flight produced sounds of approximately 41 db measured at half an inch from the source and of 449 to 603 c/s. The flight sound of the female attracted the male at distances up to 10 inches.

The fundamental tone alone trapped as many male mosquitoes as the complete flight sound of the female. Male mosquitoes were trapped on approach to favourable sounds in the presence of considerable background noise; only when this was over 100 times the favourable sound was the attraction appreciably reduced. When two or more attractive sounds were present at the same intensity there was little or no response, but as the disparity of intensity was increased, the response increased.

Recorded flight sounds of other species, when brought to the same frequency as that of the females of *A. aegypti*, were equally effective in producing an approach reaction in the males of *A. aegypti*.

Warble modulation (variation of the intensity) and vibrato modulation (variation of the frequency) of otherwise attractive sounds, if rapid (about 10 per second), decreased the attraction of the sounds.

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Book Review

Insects and Mites of Western North America. By E. O. Essig, xiv + 1050 pp., 766 figs. The Macmillan Company. 1958. Price $18.00.

This book, as stated in the title-page, is a revised edition of Professor Essig's well-known manual published in 1926 under the title *Insects of Western North America*. In his preface to the new edition Professor Essig emphasizes the revolutionary changes that have taken place in entomology since the first appearance of the book. Unfortunately the revised edition does not do justice to, and indeed hardly suggests, these changes. The original pagination is preserved unaltered. A survey of the first 100 pages shows revisions on 28 pages; of these revisions only seven are substantive: in three places obsolete control recommendations (and in one of these also a key) have been omitted and have been replaced with "filler" – on p. 44 the result is unfortunate, as a new Fig. 27 has been inserted, without, however, removing or renumbering the old Fig. 27 on the following page – on p. 7 records of five centipedes described from California have been inserted; on p. 28 some modern acaricides are briefly listed, mostly under trade names; on p. 49 a three-line account of an American mite has been substituted for a two-line account of an exotic one; on pp. 73 and 74 the passage on the control of grasshoppers has been rewritten and expanded, quoting experience up to 1952, by a collaborator, Mr. J. R. Dutton. The remaining changes in these 100 pages are mainly in names; here, too, the results are sometimes unfortunate: several names are changed in one place but not changed in another; on p. 37 the family Pyemotidae is separated from the Tarsonemidae, but the species exemplifying Pyemotidae is cited as *Tarsonemus assimilis* Banks; on p. 72 the

name of the locust mite is cited as *Pediculus rostratus* (Scopoli). In these 100 pages a rough count shows 268 references to literature; of these, 190 are to publications dated before 1916, 77 to publications from 1916 to 1925, and only one to a paper published since 1925, when *Insects of Western North America* first appeared. Five references given in the first edition have been omitted. This sample of 100 pages is probably a more than fair one, as it includes the Acarina, in which there has been more attempt to revise than in most of the major groups. In Trichoptera, for instance, there has been no change in the text, despite the complete transformation in our knowledge of this order that has resulted from the work of H. H. Ross, Betten, Milne, Denning, Schmid and others; the obsolete keys to families on the basis of adults and larvae have not been replaced; a virtually worthless list of old names of western species has been permitted to stand, occupying three pages that might well have been used for summaries of recent work and up-to-date references. In the economically important order Neuroptera there has likewise been no change despite the tremendous advances that have been made in the study of this group in the last 30 years. In the Lepidoptera some minor revisions have been made; the names of butterflies have been altered to accord partially with modern concepts; the names of moths have mostly been left unchanged, though the name of the corn earworm has been changed on p. 679 (but not on p. 681); there have been some changes in illustrations of Lepidoptera, sometimes to take up space to replace old-fashioned control recommendations, e.g., on p. 579, where Fig. 553b has been inserted (there is no 553a); as elsewhere in the book, errors and misprints are carried over from the first edition – on p. 648 a swallowtail larva is figured as that of Lorquin's admiral, on p. 681 *Agrotis ypsilon* is figured as *Lycophotia margaritosa* and *Lycophotia margaritosa* as *Euxoa messoria*, on p. 657 Nepticulidae still appears as "Nepticuilidae" in Couplet 51, and *agrestis* still as "*agresits*" on p. 682. It would be futile to multiply instances. Time has not dealt kindly with the type, and worn or broken letters are distressingly frequent; some of these appear in the 1929 printing that I have at hand, but most are new.

Despite its many faults and the perfunctory nature of the present attempt at revision, this book retains those virtues of the first edition that have not been eroded by time. The text is unusually comprehensive in scope and is clear and vivid in presentation; the references to early literature are very full; and the illustrations, most of which are original, are almost invariably good and often of striking quality. It fills a niche occupied by no other work, and if used with caution and in conjunction with more modern literature it will prove to be an invaluable source of information. What we badly need is a new and thorough revision, checked by specialists in the many fields on which the book impinges; such a revision would indeed achieve the aim that Professor Essig sets forth on the title page: "A manual and textbook for students in colleges and universities and a handbook for county, state and federal entomologists and agriculturists as well as for foresters, farmers, gardeners, travelers, and students of nature."

EUGENE MUNROE

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